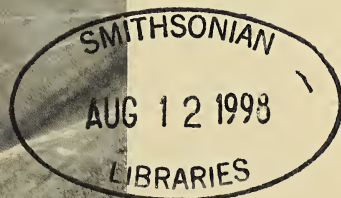# The Journal of
ARACHNOLOGY

OFFICIAL ORGAN OF THE AMERICAN ARACHNOLOGICAL SOCIETY

VOLUME 26   **1998**   **NUMBER 1**

THE JOURNAL OF ARACHNOLOGY

The Journal of Arachnology (ISSN 0160-8202), a publication devoted to the study of Arachnida, is published three times each year by *The American Arachnological Society*. **Memberships (yearly)**: Membership is open to all those interested in Arachnida. Subscriptions to *The Journal of Arachnology* and *American Arachnology* (the newsletter), and annual meeting notices, are included with membership in the Society. Regular, $30; Students, $20; Institutional, $80 (USA) or $90 (all other countries). Inquiries should be directed to the Membership Secretary (see below). **Back Issues**: Patricia Miller, P.O. Box 5354, Northwest Mississippi Community College, Senatobia, Mississippi 38668 USA. Telephone: (601) 562-3382. **Undelivered Issues**: Allen Press, Inc., 1041 New Hampshire Street, P.O. Box 368, Lawrence, Kansas 66044 USA.

THE AMERICAN ARACHNOLOGICAL SOCIETY

Cover: Tetragnatha mating, Gainesville, Florida. Photo taken with 50mm F3.5 macro mounted on telescoping extension tube and flash. Kodak Kodachrome 64 film. Photo by Joe Warfel.

Publication date: 30 July 1998

REDESCRIPTION OF *COMPSOBUTHUS MATTHIESSENI* (SCORPIONES, BUTHIDAE) FROM SOUTHWESTERN ASIA

W. David Sissom: Department of Life, Earth, and Environmental Sciences, West Texas A & M University, WTAMU Box 808, Canyon, Texas 79016–0001 USA

Victor Fet: Department of Biological Sciences, Marshall University, Huntington, West Virginia 25755–2510 USA

ABSTRACT. The buthid scorpion *Compsobuthus matthiesseni* (Birula 1905) is redescribed (male lectotype here designated), based on study of type specimens and other material now available. Its placement in the genus *Compsobuthus* Vachon 1949 is discussed, and it is regarded as a valid species of the *C. acutecarinatus* group despite possessing some unique features. In particular, its elongated pedipalps and metasoma serve to readily distinguish it from other *Compsobuthus* thus far known in the region. *Compsobuthus matthiesseni* is known from a number of localities in Iran, Iraq and Turkey. Some details of the early collections made in southwestern Asia are provided.

The scorpion *Buthus acutecarinatus matthiesseni* was described by Birula in 1905 from several localities in Persia (see below for the detailed discussion). This taxon received some attention in the literature in succeeding years. Birula (1917, 1937) listed it for western Iran along with related forms from the Middle East and North Africa. These were treated as subspecies of *B. acutecarinatus* Simon 1882, but are currently recognized as separate species of the genus *Compsobuthus*. Vachon (1949) was the first to elevate *C. matthiesseni* to species status. However, the taxonomic situation has remained unclear. Levy, Amitai & Shulov (1973) expressed doubts about the generic affiliation of this species, but tentatively included it as a good species in the acutecarinatus group. Kinzelbach (1985), for reasons unstated, considered all of the species in the *acutecarinatus* group, including *C. matthiesseni*, as subspecies of *Compsobuthus acutecarinatus*. This opinion was again published by Vachon & Kinzelbach (1987). Kovařík (1996) once again elevated *matthiesseni* to species-level status.

Some of the general problems in taxonomy of Middle Eastern scorpions are due to inadequate descriptions of species and the lack of illustrations, particularly of type materials. The inaccessibility of types led many previous workers to produce varying interpretations of species, which in turn produced great uncertainty as to their true identities and geograph-

ical distributions. Although the original description of *Buthus acutecarinatus matthiesseni* by Birula (1905) is relatively thorough, it is our goal here to update that description and to discuss the placement of *matthiesseni* in the genus *Compsobuthus* Vachon. This was made possible through the courtesy of the Zoological Institute of Russian Academy of Sciences, St. Petersburg, Russia (ZISP), which allowed us to examine a number of Birula's type specimens. The species is illustrated in detail for the first time from the type material. Detailed measurements of male and female types are presented, along with a morphometric analysis of all samples examined.

Compsobuthus matthiesseni (Birula 1905)
(Figs. 1–10)

Buthus acutecarinatus matthiesseni Birula 1905: 140 (key), 142–144; Birula 1917:140; Birula 1937:107.

Buthus (Buthus) acutecarinatus matthiesseni Birula 1918:25–27.

Compsobuthus Mathiesseni (sic): Vachon 1949:99; 1952:219.

? *Buthus acutecarinatus* var. *judaicus*: Whittick 1955: "2" (no actual pagination given).

Compsobuthus mathiesseni (sic): Pringle 1960:77.

Compsobuthus matthiesseni: Vachon 1966:211; Habibi 1971:43; Farzanpay 1988: 37; Kovařík 1996: 53–54.

Buthus acutecarinatus (part): Whittick 1970:5 (Baghdad record only).

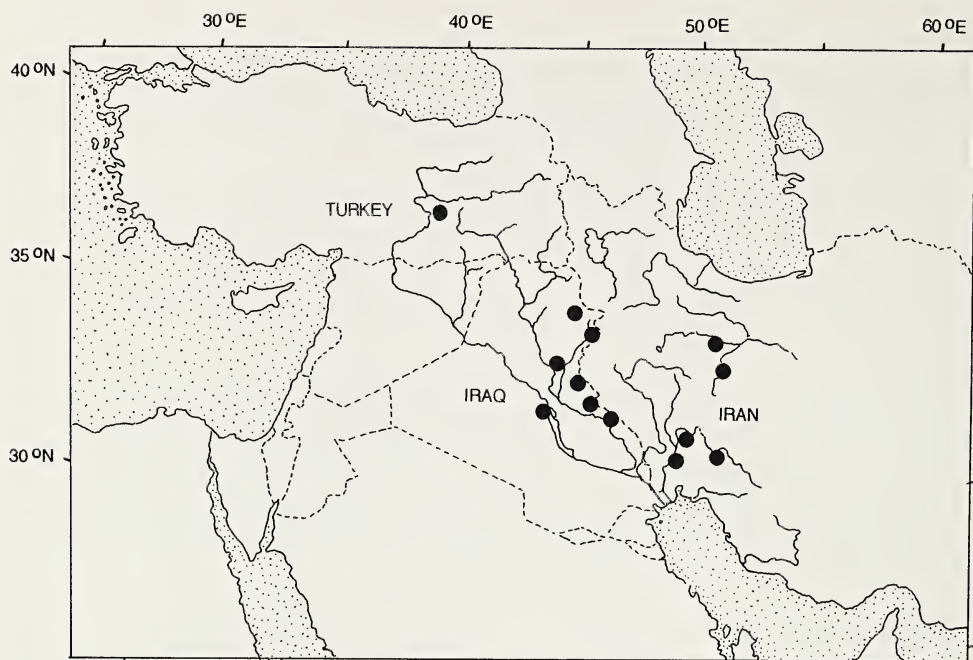*Compsobuthus* (?) *matthiesseni*: Levy, Amitai &

Figure 1.—Map of the Tigris-Euphrates drainage in Iran, Iraq, and Turkey showing distribution of *Compsobuthus matthiesseni*.

Shulov 1973:114, 115; Levy & Amitai 1980:60, 62.

Compsobuthus acutecarinatus matthiesseni: Kinzelbach 1985: map III; Vachon & Kinzelbach 1987: 101.

Type data.—Lectotype male and paralectotype female (herein designated) of *Buthus acutecarinatus matthiesseni* taken from "Prov. Iraq-Adshemi, die Stadt Kum", now Qum (Qom) in Markazi (Central) Prov., Iran, on 16 March 1904 by A. Matthiessen; deposited in ZISP, examined.

Distribution.—This species is known from a considerable number of localities in southwestern Iran, Iraq and southeastern Turkey (Fig. 1). Specimens listed by Birula (1905) were collected in 1904 by A. Matthiessen, who was a mining engineer, and the famous Russian zoologist Nikolai A. Zarudny. We analyzed Zarudny's travelogues and corresponding maps from the ZISP library, and were able to trace all of the localities of his collections. Birula's type series, collected by A. Matthiessen on 16 March 1904, originate from Kum (now Qum, or Qom). Zarudny's trips in 1903–1904 were concentrated along the Karun River valley, between Esfahan and Ahvaz. This area includes the following localities listed by

Birula (1905: 142): Disful (now Dezful); Deh-i-Dis (now Dehdez, 150 km NE from Ahvaz); Cheshme-Rogan Spring; Karavansarai Ser-i-Pul, next to the village of Malamir (now Izeh in modern Khuzestan Province); and a locality between the villages of Sarhun (now Serhun) and Gamdalkal (modern Chahar Mahal and Bakhtiari Province). Another specimen was collected by Zarudny at Nasrabad, a village next to the town of Kashan (Esfahan Province). Additional specimens from Iran were collected in 1964 by J. Neal next to Qasr-e-Shirin (modern Bakhtaran Province), close to the Iraqi border (USNM collection).

Birula (1918) described further material (2♂2♀) from Lower Mesopotamia (now Iraq) collected by P.V. Nesterov in the spring of 1914. The itinerary of this expedition is well detailed in Birula (1918: 2–6); part of its route passed from Basra (now Al-Basrah) and Amara (now Al-Amarah) along the Iranian border to the north of the Tigris River toward Mandali and Baghdad. *Compsobuthus matthiesseni* was found in the valleys of the rivers Tyb and Gengir and also next to the villages of Siaret-Seid-Hassan and Mendeli (now Mandali) (Birula 1918: 25).

Pringle (1960) lists the species from Bagh-

dad, Khanaqin, and Kirkuk in Iraq. His specimens were not examined, but were determined by Max Vachon. Kinzelbach (1985) did not include any locations from Iran, but his map shows Baghdad and a location in the Euphrates valley, close to Babylon. Kovařík (1995) confirms the species for Baghdad, and also lists the first locality in Turkey (Ergani, Diyarbakir Province). Therefore, *C. matthiesseni* appears to be distributed quite widely within the drainages of the Tigris and Euphrates Rivers and some adjacent areas in Iran, Iraq and Turkey, approximately between 30–37°N and 39–51°E.

Diagnosis.—This species, with its slender body and elongated metasoma and pedipalps, is quite distinct compared to other species of *Compsobuthus* (see Discussion), and it cannot be readily confused with any that are currently described. Within the *acutecarinatus* group, the only species to exhibit considerable elongation of the pedipalps is *C. acutecarinatus*, but its chela length/width ratio only ranges from 5.47–6.06 (in *C. matthiesseni*, male ratios range from 6.74–7.56 and female ratios from 6.18–7.00). In comparison to *C. matthiesseni*, it also has more robust metasomal segments, distinctly greater body size (40–50 mm), higher pectinal tooth counts (males with 27–29 teeth, females 20–23), a broader telson, and fused central median and posterior median carapacial carinae. *Compsobuthus longipalpus* Levy, Amitai & Shulov 1973 from the Sinai Peninsula has elongated pedipalps (chela length/width > 6.5), but has a metasoma of more typical proportions. Further, unlike *C. matthiesseni*, it is a member of the *werneri* group (with outer accessory denticles on the pedipalp chela fingers).

Redescription of lectotype.—Adult male 37.60 mm in length. Coloration: Base color light yellow, immaculate except for black pigment surrounding median and lateral eyes. *Prosoma:* Carapace slender, almost parallel-sided (Fig. 2). Ocular tubercle situated at anterior ⅓ of carapace. Anteromedian carinae weak to moderate, granulose; superciliary carinae strong, regularly denticulate; lateral ocular, central lateral, central median, and posterior median carinae moderate, irregularly denticulate. Posterior median carinae terminating distally in a small spinoid process that extends slightly beyond the posterior margin of the carapace. Central median and posterior

median carinae slightly separated by a small space, but linearly arranged as in other *Compsobuthus*. Intercarinal spaces with dense fine and coarse granulation. *Mesosoma:* Tergite I with lateral carinae moderate, denticulate and on II-VI strong, denticulate; each carina terminates in a spinoid process that extends well past the posterior margin of the tergite. Median carina moderate on I, strong on II-VI; on III-VI terminating distally in a spinoid process that terminates slightly beyond tergal margin. Lateral intercarinal spaces densely, coarsely granular; median intercarinal spaces more finely granular to shagreened. Tergite VII pentacarinate: lateral pairs strong, serrate; median carina present only on proximal one-half, strong, serratocrenulate. Pectinal tooth count 23–22. Sternite III moderately hirsute; others less so. Lateral carinae absent on sternite III, faint to weak and smooth on IV-VI, strong and serrate on VII. Submedian carinae absent on sternites III-VI; moderate and finely serrate on VII. *Metasoma:* All segments elongated (Fig. 3), with segment III length/width ratio, 2.84 and V length/width ratio, 3.93; segments III-V virtually parallel-sided. Segments I-IV: Dorsolateral and lateral supramedian carinae strong, finely, irregularly serrate. Lateral inframedian carinae on I strong, finely serrate; on II represented by a weak line of granules in anterior third, and as a moderate keel on posterior two-thirds, this finely crenulate to serrate; on III indicated by a faint line of small isolated granules; on IV absent. Ventrolateral carinae on I-IV strong, finely crenulate. Ventral submedian carinae moderate, very finely serrate; these carinae provided on each segment with three pairs of setae with the third pair at the distal edge of the segments. Dorsal and lateral intercarinal spaces with scattered coarse granulation; ventral surfaces shagreened. Segment V with dorsolateral carinae moderate, serrate; lateromedian carinae indicated by an irregularly-spaced row of coarse granules; ventrolateral and ventromedian carinae strong, crenulate with the granules gradually increasing in size toward distal end. All intercarinal spaces moderately coarsely granular. *Telson:* Ventral aspect with median and paired lateral rows of rounded granules; subaculear tubercle indicated by an elevated, rounded area when viewed from lateral aspect; aculeus gently curved and relatively short (Fig. 3). *Pedipalps:* Trichobothrial pattern

Type A, orthobothriotaxic (Vachon 1974); dorsal trichobothria of femur arranged in beta-configuration (Vachon 1975). Femur (Fig. 4) slender (length/width = 4.35), pentacarinate, with all carinae moderate, more or less crenulate; inner face moderately granular with irregular oblique longitudinal keel; dorsal and ventral faces moderately granular; two short distal external accessory macrosetae. Patella (Fig. 5) octocarinate, with dorsointernal carina moderate, granular; dorsal median carina weak, granular; dorsoexternal carina weak, finely granular; exteromedian carina moderate, essentially smooth; ventroexternal carina weak, finely granular; ventromedian carina weak, smooth; ventrointernal and inner carinae strong, serrate. Patella without accessory macrosetae. Chela (Figs. 6–10) palm very slender with chela length/width ratio, 6.74; dorsal marginal and ventroexternal carinae weak, granular; other carinae of outer palm surface faint, feebly granular. Chela fingers long and tenuous, with ratio of fixed finger length/carapace length, 1.08. Fixed and movable chela fingers with 10 oblique rows of denticles (Figs. 8–9), these lacking outer accessory denticles; movable finger with 4 distal granules preceding first granular row (Fig. 10). Fixed finger trichobothria *et* opposite extreme distal end of fourth granular row, *est* opposite enlarged granule at base of fifth row (Fig. 7).

Measurements of lectotype male (mm): Total L, 37.60; carapace L, 3.70; mesosoma L, 11.45; metasoma L, 22.45; telson L, 3.85. Metasomal segments: I L/W, 3.60/1.85; II L/W, 4.20/1.60; III L/W, 4.40/1.55; IV L/W, 4.95/1.70; V L/W, 5.30/1.35. Telson: vesicle L/W/D, 2.45/1.20/1.70; aculeus L, 1.40. Pedipalps: femur L/W, 3.70/0.85; patella L/W, 4.20/1.10; chela L/W/D, 6.40/0.95/1.05; fixed finger L, 4.00; movable finger L, 4.50; palm (underhand) L, 2.05.

Measurements of paralectotype female (mm): Total L, 43.95; carapace L, 4.75; mesosoma L, 12.75; metasoma L, 22.00; telson L, 4.45. Metasomal segments: I L/W, 3.55/2.35; II L/W, 4.05/2.10; III L/W, 4.30/2.10; IV L/W, 4.75/2.00; V L/W, 5.35/1.90. Telson: vesicle L/W/D, 2.65/1.65/1.60; aculeus L, 1.80. Pedipalps: femur L/W, 4.25/1.10; patella L/W, 4.90/1.55; chela L/W/D, 7.55/1.15/1.30; fixed finger L, 4.85; movable finger L, 5.55; palm (underhand) L, 2.20.

Variation.—Juveniles bear some dusky pigmentation on the carapacial and tergal carinae, as well as the proximal portion of the fifth metasomal segment. Interestingly, the juveniles have fairly similar morphometrics to the adults, and males and females are distinguishable in the middle instars. It is highly likely that individuals mature at different instars, as is known to be the case in a number of other scorpions (e.g., *Centruroides* Marx 1889; Francke & Jones 1982).

For all adult specimens examined, morphometric variation is summarized in Tables 1 and 2. Note that females differ from males in having the metasomal segments more robust. The non-type male specimens all had proportionately longer metasomal segments than the lectotype, which is illustrated (Fig. 3). Pectinal tooth counts varied as follows: in males, 1 comb with 20 teeth, 5 combs with 21 teeth, 5 combs with 22 teeth, 15 combs with 23 teeth, 6 combs with 24 teeth, and 1 comb with 25 teeth; in females, 1 comb with 17 teeth, 2 combs with 18 teeth, 13 combs with 19 teeth, 20 combs with 20 teeth, and 7 combs with 21 teeth. The dentition of the right chela fingers in 20 specimens was also examined, and the fixed finger bore either nine (5%), 10 (85%) or 11 (10%) oblique rows of denticles; the movable finger bore either 10 (35%) or 11 rows (65%). In those specimens having eleven rows on the movable finger, the denticle at the base of the finger that separated the tenth and eleventh rows (= the enlarged granule at the base of the tenth denticle row) was generally smaller than the enlarged denticles separating other rows. When this denticle was the same size as the other denticles in the row, the two basal rows were fused into a single long row and the specimen was judged to have only 10 total rows.

Specimens examined.—IRAN: *Markazi (Central) Prov.*, Qom (Qum), 16 Mar 1904 (A. Matthiessen), 1♂ (lectotype), 1♀ (paralectotype) (ZISP, No. 53); *Chahar Mahal and Bakhtiari Prov.*, between villages Sarkhun (Serhun) and Gamdalkal, 16 km NEE Dehdez, 9–10 April 1904 (N.A. Zarudny), 2♀ (paralectotypes) (ZISP, No. 58); *Khuzestan Prov.*, Dezful, 10 March 1904 (N.A. Zarudny), 4♀ (ZISP, No. 54); *Bakhtaran (Kermanshah) Prov.*, 8 km E Qasr-e-Shirin, 15 April 1964 (J. Neal), 1 juv.♀ (USNM), 3♂, 2 juv.♂, 3♀, 6 juv.♀ (USNM). IRAQ: *Baghdad Prov.*, Baghdad, November 1934–April 1935 (Yusaf Lazar), 1♂2♀ (FMNH); Bagh-

Table 1.—Means ($\bar{x}$), standard deviations (SD), and ranges (min = minimum, max = maximum values) for selected measurements of *Compsobuthus matthiesseni,* based on 13 adult males and 16 adult females. Measurements are as follows: Ca L = carapace length; Fem L = pedipalp femur length; Fem W = pedipalp femur width; Ch L = pedipalp chela length; Ch W = pedipalp chela width; FF L = pedipalp chela fixed finger length; MF L = pedipalp chela movable finger length; III L = metasomal segment III length; III W = metasomal segment III width; V L = metasomal segment V length; V W = metasomal segment V width.

	Ca L	Fem L	Fem W	Ch L	Ch W	FF L	MF L	III L	III W	VL	VW
Males											
$\bar{x}$	3.73	3.71	0.86	6.33	0.89	4.00	4.48	4.42	1.47	5.32	1.28
SD	0.31	0.33	0.07	0.63	0.09	0.35	0.41	0.46	0.16	0.51	0.14
min	3.30	3.20	0.75	5.05	0.70	3.50	3.90	3.65	1.20	4.50	1.00
max	4.30	4.35	1.00	7.45	1.00	4.80	5.30	5.25	1.80	6.25	1.55
Females											
$\bar{x}$	4.19	3.80	1.02	6.76	1.02	4.37	4.96	3.73	1.80	4.66	1.64
SD	0.44	0.38	0.10	0.63	0.10	0.42	0.48	0.39	0.23	0.49	0.23
min	3.50	3.10	0.85	5.65	0.85	3.65	4.05	3.05	1.45	3.85	1.30
max	4.75	4.25	1.15	7.55	1.15	4.95	5.60	4.30	2.10	5.35	1.90

dad, 1940–42 (coll. unknown), 9♂4♀ 1 juv.♂, 1 juv.♀ (collections of the authors).

DISCUSSION

With regard to the generic placement of this species, Levy, Amitai & Shulov (1973) questioned whether or not it belonged in the genus *Compsobuthus,* based on its atypical carapacial carination, with the central median and posterior median carinae not completely fused, its elongated metasoma, and the shape of its telson. Although the carapacial carinae are not fused, they are in a linear arrangement (Fig. 2) as in other *Compsobuthus.* In addition, the terminal spines of these carinae and the three carinae of the tergites do not protrude as far beyond the posterior margins of the carapace and tergites, respectively, as in other *Compsobuthus,* but are nevertheless distinct.

The illustration by Pringle (1960: 77) indicates enlarged denticles at the distal end of the ventrolateral carinae of metasomal segment V. This may merely represent an error in illustrating the specimen. The type specimens, as well as non-type specimens from Baghdad that we examined, do not exhibit this feature; the keels are more or less evenly crenulated from anterior to posterior, as in other *Compsobuthus.* Otherwise, Pringle's illustration is consistent with *C. matthiesseni.*

We do not attach great significance to the

Table 2.—Means ($\bar{x}$), standard deviations (SD), and ranges (min = minimum, max = maximum values) for selected morphometric ratios of *Compsobuthus matthiesseni,* based on 13 adult males and 16 adult females. Ratios are based on the same abbreviations listed in Table 1.

	Ch L/W	FF L/ChL	FF L/Ca L	MF L/V L	III L/W	V L/W	Fem L/W
Males							
$\bar{x}$	7.10	0.63	1.07	0.84	3.02	4.18	4.33
SD	0.24	0.02	0.02	0.03	0.20	0.30	0.10
min	6.74	0.61	1.04	0.79	2.70	3.75	4.12
max	7.56	0.69	1.12	0.90	3.46	4.70	4.50
Females							
$\bar{x}$	6.67	0.65	1.04	1.07	2.07	2.85	3.72
SD	0.44	0.38	0.10	0.63	0.10	0.42	0.48
min	6.18	0.63	0.98	0.98	1.98	2.63	3.44
max	7.00	0.66	1.13	1.15	2.26	3.18	3.90
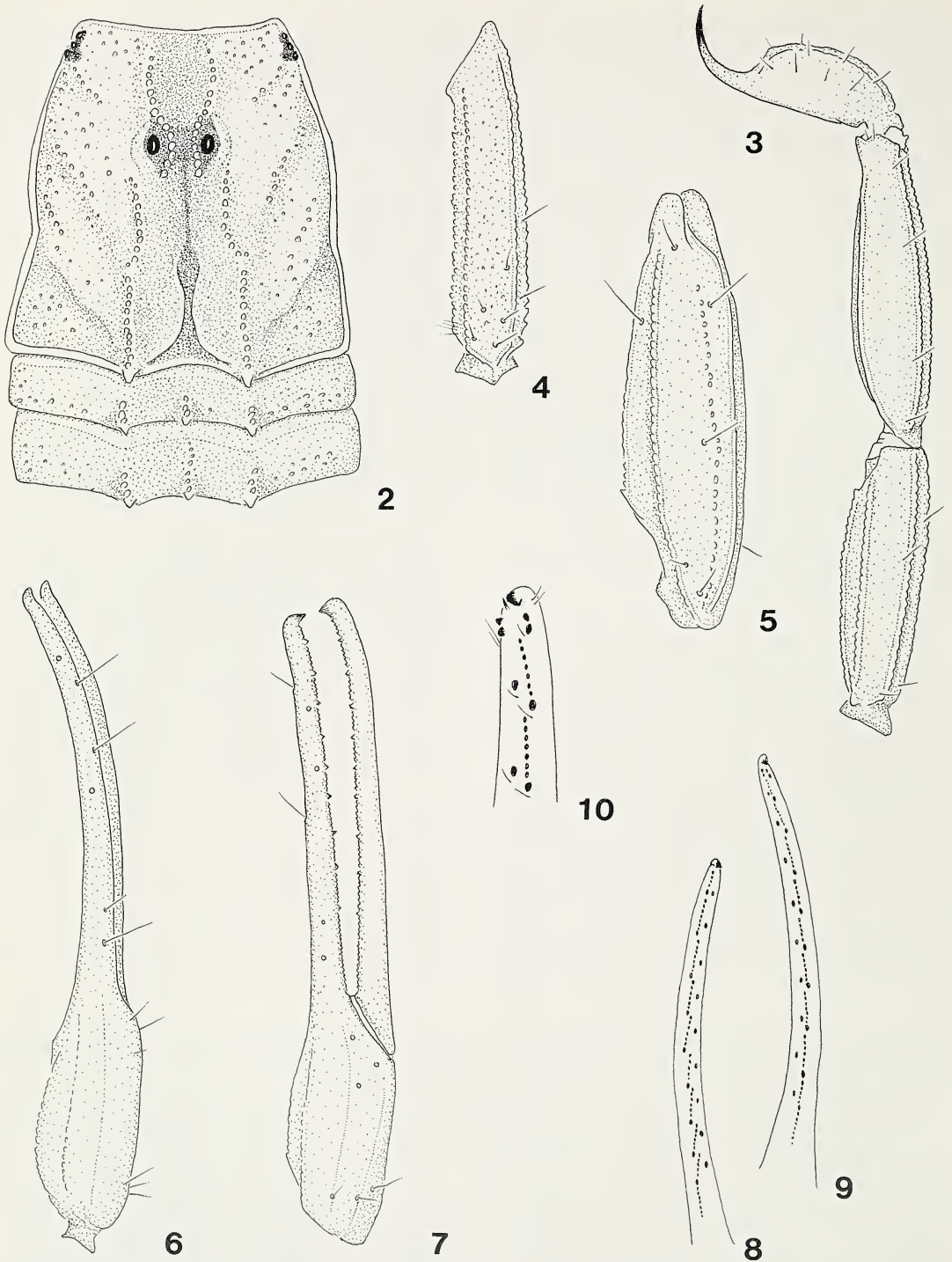
Figures 2–10.—Morphology of *Compsobuthus matthiesseni* (all drawings of lectotype male), except as indicated. 2, Dorsal aspect, showing carapace and first two tergites; 3, Lateral view of metasomal segments IV and V and the telson; 4, Dorsal aspect of pedipalp femur; 5, Dorsal aspect of pedipalp patella; 6, Dorsal aspect of pedipalp chela; 7, External aspect of pedipalp chela; 8, Dentition of pedipalp chela fixed finger; 9, Dentition of pedipalp chela movable finger; 10, Enlargement of distal end of pedipalp chela movable finger.
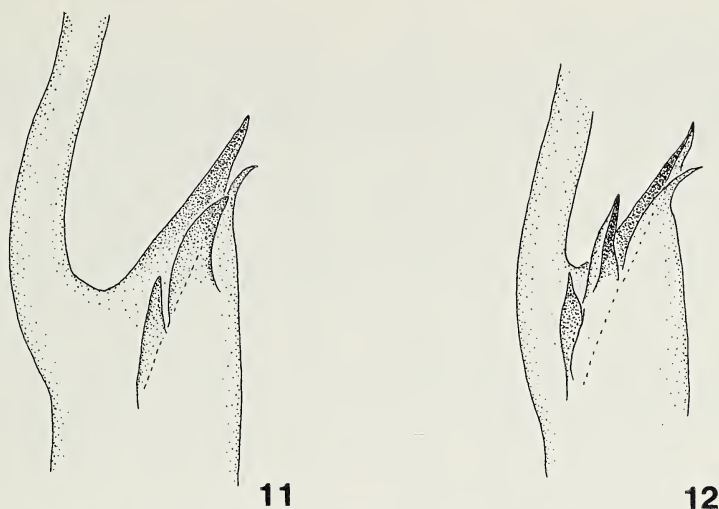
Figures 11–12.—Morphology of the hemispermatophore of *Compsobuthus matthiesseni* (non-type male from Baghdad). 11, Dorsal aspect of right hemispermatophore, showing arrangement of lobes at base of flagellum; 12, Right hemispermatophore from ental-dorsal angle (terminology after Lamoral 1979).

elongation of the metasomal segments in this species as a possible character of generic importance, although we consider it an exceptional species character. In the New World genus *Centruroides* for example, most species have elongated metasomal segments (particularly in the male), but there are notable exceptions in which dimorphism in metasoma length is greatly reduced [e.g., *C. testaceus* (DeGeer 1778), *C. exsul* (Meise 1934), *C. rileyi* Sissom 1995]. Interspecific differences in the occurrence of sexual dimorphism in metasoma length, as well as in the degree of dimorphism, are also known in *Uroplectes* Peters 1861 in southern and eastern Africa, *Isometrus* Hemprich & Ehrenberg 1829 in Africa and Asia, *Tityus* C.L. Koch 1836 in Central and South America, and others. The slenderness of the telson is also distinctive in *C. matthiesseni*—however, this is most notable in the male and is not unique to this species. In general, those species with more slender metasomal segments will have more slender telsons; the presence or absence, as well as the shape, of the subaculear tubercle is also not exceptional. *Compsobuthus vachoni* Sissom 1994 has a larger subaculear tubercle than that seen in *C. matthiesseni*.

Finally, we were able to dissect the hemispermatophore of this species. The basic structure, including the arrangement of the lobes at the base of the flagellum (Figs. 11–12), is consistent with that found in other *Compsobuthus*, as illustrated in several species by Levy & Amitai (1980). In conclusion, we feel that *C. matthiesseni* is clearly related to the other species in the genus and appropriately belongs in *Compsobuthus*.

Kinzelbach (1985) and Vachon & Kinzelbach (1987) placed *C. matthiesseni* once again as a subspecies of *Compsobuthus acutecarinatus*. This scorpion is quite distinct from *C. acutecarinatus* (see Diagnosis), and it is our opinion that the taxonomic arrangement proposed by Levy, Amitai & Shulov (1973), with *C. matthiesseni* as a valid species in the *acutecarinatus* group, is more appropriate. Additional comments on the species groups of *Compsobuthus* to this effect have been published elsewhere (Sissom 1994).

ACKNOWLEDGMENTS

phometric and meristic variation. Jonathan Coddington of the United States National Museum (USNM), Washington, D.C. and Daniel Summers of The Field Museum, Chicago (FMNH) provided the additional specimens included in this study. We would also like to give a special thanks to Tom Anton, research assistant of the Field Museum, for bringing to our attention the specimens from that Museum. Graeme Lowe of the Monell Chemical Senses Center, Philadelphia read the manuscript and made important suggestions and corrections, derived from his own notes on the species. Kari J. McWest and Chad M. Lee of West Texas A & M University also commented on a draft of the manuscript. Mark Volkovich (ZISP) kindly supplied us with information on N.A. Zarudny's field trips found in ZISP library.

LITERATURE CITED

Birula, A. 1905. Beiträge zur Kenntniss der Skorpionenfauna Persiens. (Dritter Beitrag). Bull. Acad. Imp. Sci. St.-Pétersbourg, ser. 5, 23 (1–2): 119–148.

Birula, A. 1917. Fauna of Russia and adjacent countries. Arachnoidea. Vol. I. Scorpiones. Israel Program for Scientific Translations, Jerusalem, 1965.

Birula, A. 1918. Miscellanea scorpiologica. XI. Materials on the scorpion fauna of Outer Mesopotamia, Kurdistan, and North Persia. Annuaire Mus. Zool. Acad. Sci. Petrograd, 27:1–44. (in Russian).

Birula, A.A. 1937. Notes sur les collections de scorpions recueillis dans le Jémen (Arabie S.E.). Arch. Mus. Zool. Univ. Moscou, 4:101–110 (in Russian).

Farzanpay, R. 1988. A catalogue of the scorpions occurring in Iran, up to January 1986. Revue Arachnol., 8(2):33–44.

Francke, O.F. & S.K. Jones. 1982. The life history of *Centruroides gracilis* (Scorpiones, Buthidae). J. Arachnol., 10:223–239.

Habibi, T. 1971. List de scorpions de l'Iran. Bull. Faculty of Science, Tehran Univ., 2(4):42–47.

Kinzelbach, R. 1985. Vorderer Orient. Skorpione (Arachnida: Scorpiones). Tübinger Atlas des Vorderen Orients (TAVO), Karte Nr. A VI 14.2. Tübingen.

Kovařík, F. 1996. First report of *Compsobuthus matthiesseni* (Scorpionida: Buthidae) from Turkey. Klapalekiana, 32:53–55.

Lamoral, B.H. 1979. The scorpions of Namibia

(Arachnida: Scorpionida). Ann. Natal Mus. 23(3):497–784.

Levy, G. & P. Amitai. 1980. Fauna Palaestina. Arachnida I. Scorpiones. Israel Acad. Sci. Hum., Jerusalem, 130 pp. + 1 map.

Levy, G., P. Amitai & A. Shulov. 1973. New scorpions from Israel, Jordan and Arabia. Zool. J. Linn. Soc., 52:113–140.

Pringle, G. 1960. Notes on the scorpions of Iraq. Bull. Endemic Diseases, Baghdad 3(3–4):73–87.

Sissom, W.D. 1994. Descriptions of new and poorly known scorpions of Yemen (Scorpiones: Buthidae, Diplocentridae, Scorpionidae). Fauna of Saudi Arabia, 14:3–39.

Vachon, M. 1949. Études sur les Scorpions. III. Description des Scorpions du Nord de l'Afrique. Arch. Inst. Pasteur d'Algérie, 27(1):66–100.

Vachon, M. 1952. Études sur les Scorpions. Institut Pasteur d'Algérie, Alger. 482 pp.

Vachon, M. 1966. Liste des scorpions connus en Égypte, Arabie, Israël, Liban, Syrie, Jordanie, Turquie, Irak, Iran. Toxicon, 4:209–218.

Vachon, M. & R. Kinzelbach. 1987. On the taxonomy and distribution of the scorpions of the Middle East. Pp. (A) 28:91–103. *In* Proceedings of the Symposium on the Fauna and Zoogeography of the Middle East, Mainz 1985.(F. Krupp, W. Schneider & R. Kinzelbach, eds.), Beihefte zum Tübinger Atlas des Vorderen Orients.

Vachon, M. 1974. Étude des caráctères utilisés pour classer les familles et les genres de scorpions. 1. La trichobothriotaxie en Arachnologie. Sigles trichobothriaux et types de trichobothriotaxie chez les Scorpions. Bull. Mus. Nat. Hist. Nat. Paris, sér. 3, No. 140 (Zool. 104):857–958.

Vachon, M. 1975. Sur l'utilisation de la trichobothriotaxie du bras des pedipalpes des Scorpions (Arachnides) dans le classement des genres de la famille des Buthidae Simon. C.R. Acad. Sci. Paris, sér. D., 281:1597–1599.

Whittick, R. 1955. Scorpions from Palestine, Syria, Iraq and Iran. *In* Contributions to the Fauna and Flora of Southwestern Asia. (H. Field, ed.), Privately printed by Henry Field, Coconut Grove, Florida. (Miscellanea Asiatica Occidentalis XII, Amer. Document. Inst. Microf. No. 4612: 76–81).

Whittick, R. 1970. Scorpions collected by Field Museum Near East expedition, 1934. Privately printed by Henry Field, Coconut Grove, Florida.

Zaroudny, N. 1904. Itineraire de l'expedition dans la Perse occidentale en 1903–1904. A reprint from: Ann. Mus. Zool. Impér. Acad. Sci., 9, 7 pp. (in Russian).

A NEW FOSSIL HARVESTMAN FROM DOMINICAN REPUBLIC AMBER (OPILIONES, SAMOIDAE, *HUMMELINCKIOLUS*)

James C. Cokendolpher: 2007 29th Street, Lubbock, Texas 79411 USA

George O. Poinar, Jr.:   Entomology Department, Oregon State University, Cordley Hall 2046, Corvallis, Oregon 97331 USA

ABSTRACT.   *Hummelinckiolus silhavyi* new species is described from both the male and female from Dominican Republic amber (Upper Eocene in age). This is the first record of the genus from Hispaniola and the Greater Antilles. An emended diagnosis of *Hummelinckiolus* is provided. A modern *Hummelinckiolus* sp. is reported from St. John, U.S. Virgin Islands.

The traditional view of the world-wide family Phalangodidae and its subfamilies by Roewer (1923) was based entirely on characters of external morphology. More recent studies of the genitalia are revealing many of the subfamilies are polyphyletic and that most of these subfamilies should be raised to full family status. The Phalangodinae as viewed by Roewer (1923) is such a polyphyletic group. Martens (1986) and Staręga (1989) noted that the members of the Phalangodinae (Phalangodidae *sensu stricto*) are apparently restricted to the Holarctic region and that previously included taxa from other regions need revision and regrouping in other families. This revision has been completed (at least in part) but has not been published (Kury 1993). Kury (pers. comm. 1996) has examined specimens from Madagascar and illustrations of others from Australia which he deems to belong to the Phalangodidae *sensu stricto*, but otherwise the Phalangodidae appear to be limited to the Holarctic region. None of the Caribbean taxa formerly placed in the Phalangodidae remain there in Kury's revision. Some of the Caribbean "phalangodids" had previously been moved to the Samoinae by Šilhavý (1979). Staręga (1992) raised the subfamily Samoinae (Phalangodidae) to full family status; an action that is accepted by Kury (pers. comm. 1996). There are currently 22 genera placed in the Samoidae, and Kury (pers. comm. 1996) accepts an additional five genera. Of these, 12 occur in the West Indies, Central America, and Venezuela. The remaining genera are found in Africa and scattered localities in the Indian and Pacific oceans and do not have member species occurring in the Americas.

"Phalangodid" harvestmen are poorly known from Hispaniola. The present discovery of a new species brings the total for the island to eight, half of which are known only by fossils (Cokendolpher & Camilo-Rivera 1989; Cokendolpher & Poinar 1992). As noted by us earlier (1992), this apparent scarcity of species may not be a true reflection of the fauna. More likely, the low number of species is an indication of the few collections made. Although there are four fossil species of "phalangodid" recorded from the Dominican Republic, only a single modern species has been reported (Cokendolpher 1987). The "phalangodid" fauna of the Dominican Republic now consist of *Hummelinckiolus silhavyi* new species (Samoidae) †, *Kimula* sp. (Minuidae, according to Kury pers. comm. 1996) †, *Pellobunus haitiensis* Šilhavý 1979 (Samoidae), *Pellobunus proavus* Cokendolpher 1987 (Samoidae) †, and *Philacarus hispaniolensis* Cokendolpher & Poinar 1992 (Samoidae?) †.

MATERIALS

The amber pieces containing the fossils are believed to have originated from mines in the northern mountain ranges in the Dominican Republic. These mines are in the El Mamey Formation (Upper Eocene), which is shale-sandstone interspersed with a conglomerate of well-rounded pebbles (Eberle et al. 1980). The exact age of the amber is unknown. It was formed from resins produced by an extinct al-

garroba tree (*Hymenaea protera* Poinar 1991: Leguminosae). Clumps of resin fell from the trees to the ground, were buried, then washed by torrential rains, and deposited in low-lying areas. These areas were then flooded by sea water; and, later, the amber was deposited along with other sediments on the sea floor. Mountain formation resulted in the amber and other marine deposits being uplifted to the surface where it is now exposed in the mines. Estimates based on microfossils in the deposits of the Dominican Republic and chemical analyses of the ambers from various mines on the island provide a range from 15–20 million years (Iturralde-Vincent & MacPhee 1996) to 30–45 million years (Cepek in Schlee 1990).

SYSTEMATICS

Order Opiliones

Suborder Laniatores

Family Samoidae Sørensen 1886

Hummelinckiolus Šilhavý

Hummelinckiolus Šilhavý 1979:8.

Type species.—*Hummelinckiolus parvus* Šilhavý 1979, by monotypy.

Diagnosis (emended).—Ocular tubercle cone-shaped, slightly to strongly directed anteriorly, unarmed, placed on anterior edge of cephalothorax; anterolateral margin of cephalothorax with 1–2 small tubercles over each trochanter I; chelicerae not sexually dimorphic, without stridulatory organ; pedipalps without teeth, femur with distomesal spine, tibia with two pairs of ventrolateral spines; leg tarsal segments 3:(3/4):(4/5):(4/5), with scopulae on III and IV; femur IV not enlarged or armed in males; distitarsus I and II each with two segments; metatarsus III enlarged and spindleform in male; areae, free tergites and free sternites unarmed, first area without median line; spiracles not visible.

Identification.—The combination of the above mentioned diagnostic characters will separate *Hummelinckiolus* from all other known "phalangodids." The presence of three tarsal I segments will separate *Hummelinckiolus* from all New World genera currently placed in the Samoidae. Kury (pers. comm. 1996) also placed three Central and South American genera with three tarsal I segments into the Samoidae: *Cornigera* González-Spon-

ga 1987, *Microminua* Sørensen 1932, and *Neocynortina* Goodnight & Goodnight 1983. *Hummelinckiolus* and members of these genera also have similar penes: truncus not greatly widened and truncated distally, with two longitudinal rows of 3–4 dorsal spines (González-Sponga 1987, figs. 62–63; Sørensen 1932, fig. 8; Goodnight & Goodnight 1983, fig. 68; Šilhavý 1979, figs. 16–17). The members of the three Central and South American genera are not sexual dimorphic, whereas *Hummelinckiolus* differs by having the male metatarsus III enlarged and spindleform. Spindleform metatarsus III also are known from six other samoid genera and the related family Biantidae. *Hummelinckiolus* is the only New World Samoidae with 2–2 distitarsal segments; all other New World genera (including the three genera recognized by Kury) have 2–3 segments. Most, but not all, Old World samoid genera also have 2–3 segments.

Comments.—With the description of *Hummelinckiolus silhavyi* new species, the genus now contains two named species. *Hummelinckiolus parvus* Šilhavý 1979 is known for several of the smaller Windward Islands in the Lesser Antilles. *Hummelinckiolus silhavyi* new species is known only from Dominican Republic amber.

The "Samoinae gen. et sp." reported by Muchmore (1993) from St. John, U.S. Virgin Islands we also place in *Hummelinckiolus*. This species differs from the two described species by the greater number of tarsal II segments (4, instead of 3) and by having the ocular tubercle more pointed (but still rounded). These are probably insignificant differences at the generic level and therefore we have emended the generic diagnosis above to include these characters. The penis of the St. John species is very similar to that illustrated by Šilhavý (1979; figs. 16, 17) for *H. parvus*; differing mainly by having longer spines. Further description of this modern taxa is beyond the scope of this paper.

Hummelinckiolus silhavyi new species
Figs. 1–4

Type data.—The female holotype (# A-10-75A) and male paratype (# A-10-75B) are deposited in the Poinar Amber Collection maintained at the Entomology Department, Oregon State University, Corvallis, Oregon.

Etymology.—This species is named in
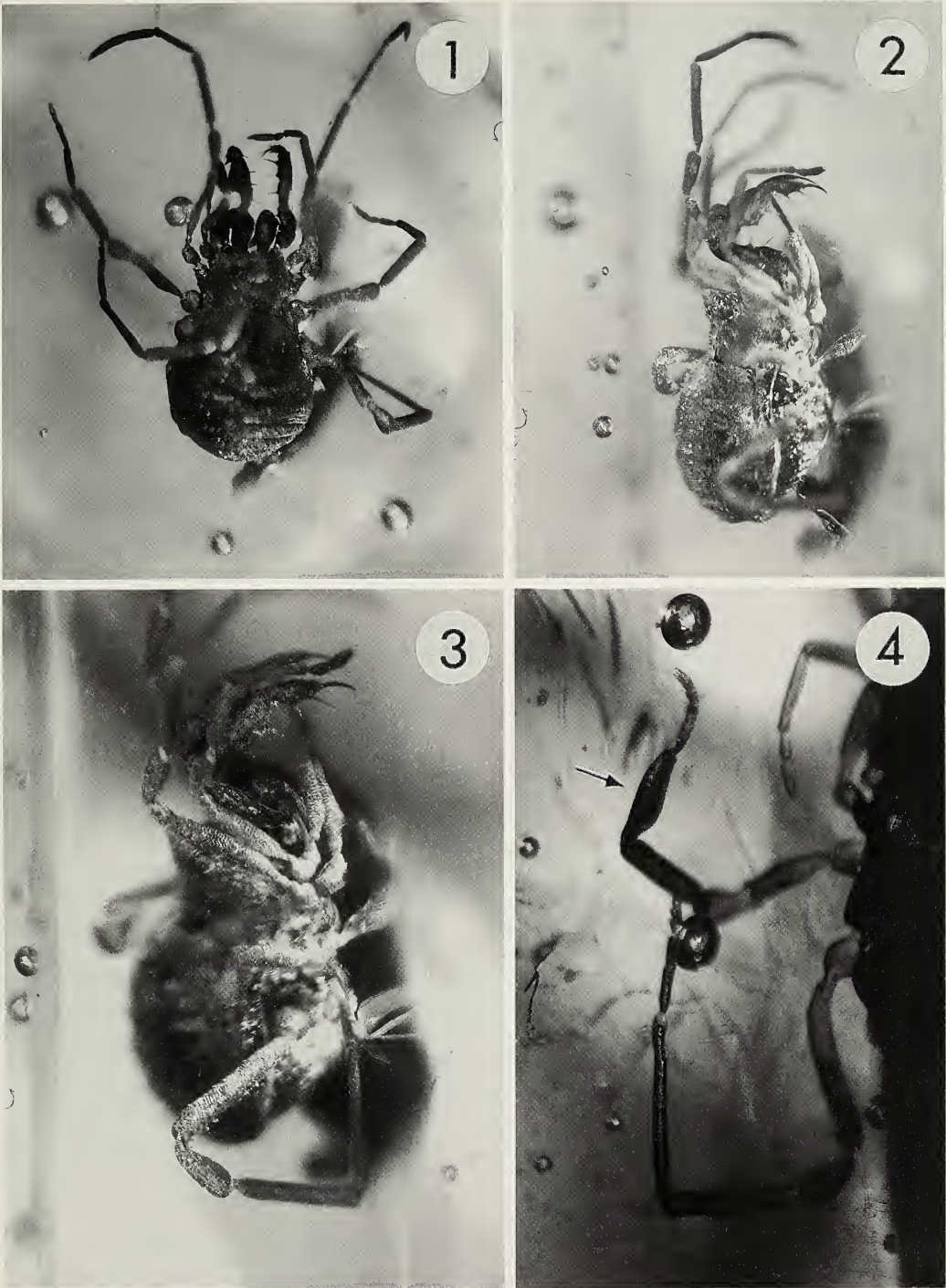
Figures 1–4.—*Hummelinckiolus silhavyi* new species. 1, Dorsal view of body, female; 2, Lateral view of body, showing ocular tubercle, female; 3, Lateral view of leg femora showing fine granulation, female; 4, Legs 3, 4, and part of leg 2, note enlarged metatarsus 3, male.

Table 1.—Appendage lengths (in mm) in **Hummelinckiolus silhavyi** new species (? = structure obviously distorted or hidden from view).

	Leg I	Leg II	Leg III	Leg IV	Palpus
Female					
Trochanter	0.13	0.12	0.12	0.16	0.12
Femur	0.50	0.58	0.52	0.70	0.40
Patella	0.16	0.28	0.20	0.30	0.22
Tibia	0.27	0.50	0.38	0.48	0.25
Metatarsus	0.29	0.80	0.46	0.69	—
Tarsus/Claw	0.34	0.55	0.34	0.47	0.45
Totals	1.69	2.83	2.16	2.74	1.44
Male					
Trochanter	0.13	0.14	0.13	0.18	0.18
Femur	?	?	0.51	0.72	?
Patella	0.23	?	0.25	0.30	0.24
Tibia	0.32	0.63	0.46	0.53	0.28
Metatarsus	0.43	0.52	0.50	0.80	—
Tarsus/Claw	0.28	0.65	0.34	0.51	0.46
Totals	1.26+	1.94+	2.19	3.04	1.16+

honor of Vladimir Šilhavý (1913–1984) for his detailed studies of West Indian opilions.

Differential diagnosis.—*Hummelinckiolus silhavyi* new species is easily distinguished from *H. parvus* on the basis of the number of tarsal segments: 3:3:5:5 in *H. silhavyi* and 3:3:4:4 in *H. parvus*. The legs of *H. silhavyi* are finely granulated, whereas those of *H. parvus* are smooth. The new species is also smaller in overall size, but the significance of this is unknown because of the small sample size.

Description.—*Female:* Body small, total length 1.38 mm, greatest width (posterior end of abdomen) 0.94 mm; cephalothorax length 0.36 mm; ocular tubercle cone-shaped, slightly anteriorly directed, unarmed, 0.10 mm tall, 0.23 mm wide at base; placed at anterior edge of cephalothorax; eyes on base of ocular tubercle; cheliceral segment lengths 0.25 mm (basal piece), 0.54 mm (distal piece, 0.26 fixed jaw); distal ⅔ of basal segment somewhat enlarged and raised dorsally; stridulatory organs absent. Dorsum of body and leg coxae covered with relatively large granules; ventrally with only a few scattered fine granules and a row of small granules on each free sternite. Genital operculum 0.16 wide, 0.16 long; with only fine granules and few setae. Anterior margin of cephalothorax with two (left) and one (right) small tubercles at base of each leg I. Openings to scent glands and spiracles undetected. Appendage lengths in Table 1.

Pedipalps with long spines: two on basomesal and one on distomesal areas of femur; patella with single spine ventromesally; tibia and tarsus each with mesal and lateral pair ventrally; tarsal claw long, smooth. Legs densely covered with fine granules, unarmed; femora IV curved to follow outline of abdomen. Tarsal segments 3:3:5:5; scopulae undetected (see comments below); tarsus IV uniform, 0.04 mm wide; distitarsus I and II each with two segments.

Male: Generally as for female, except body smaller and appendages longer. Appendage lengths in Table 1. Tarsus IV enlarged (0.11 mm wide in middle) and spindleform. Male not as well preserved and amber has cracks and air bubbles which obstruct some views. Total length 1.19 mm, greatest width 0.88 mm; ocular tubercle 0.21 wide, height obscured; chelicerae not greatly enlarged or otherwise modified. Anterior margin of cephalothorax with two (left, right view obscured) tubercles at base of leg I.

Comments.—It is remarkable that of two specimens known, each sex is represented. Modern "phalangodids" are often found together in pairs under rocks or logs. Because the amber containing the two fossils are different colors, we assume the animals were not together when entrapped in the algarroba tree resin.

Šilhavý (1979) diagnosed the Samoinae

(now regarded as the Samoidae) based in part on the belief that all species had scopulae on tarsi III and IV. No tarsal scopulae were mentioned in the original descriptions of *Cornigera*, *Microminua*, and *Neocynortina*, which Kury places in this family. Members of these genera, like *Hummelinckiolus*, are small animals (body length about 1–1.5 mm) and tarsal scopulae could have been overlooked. Kury (pers. comm. 1996) also places the *"Crosbyella"* spp. described by González-Sponga (1987) from Venezuela in the Samoidae and according to the original descriptions they do not have tarsal scopulae. The tarsal scopulae are difficult (at best) to see on the fossils reported herein. Cokendolpher (1987) remarked that the scopulae on the fossil *Pellobunus proavus* was not as dense as the other congener on that island. Goodnight & Goodnight (1983) noted that the scopulae on Central American *Pellobunus* spp. were not conspicuous and easily overlooked. It appears that the scopulae are not as dense or absent in some samoid genera. It is possible that the microtrichia of the scopulae have an optical density near that of amber, making them to appear to be reduced or absent. The scopulae on the *Hummelinckiolus* from St. John Island are visible; as are those on the type species of the genus. In the original description (Cokendolpher & Poinar 1992), *Philacarus hispaniolensis* was reported to lack scopulae. We have reexamined the fossil and confirmed its absence. In the original description of the only other species in the genus (a modern species from Colombia), Sørensen (1932) did not mention scopulae but placed the genus near *Pellobunus* Banks 1905 and *Metapellobunus* Roewer 1923 (both of which have scopulae). A special effort should me made to reveal the status of scopulae on any new material of *Philacarus*. Scopulae should also be sought on modern members of *Cornigera*, *Microminua*, *Neocynortina*, and *"Crosbyella."*

ACKNOWLEDGMENTS

LITERATURE CITED

Cokendolpher, J.C. 1987. A new species of fossil *Pellobunus* from Dominican Republic amber (Arachnida: Opiliones: Phalangodidae). Caribbean J. Sci. (1986), 22:205–211.

Cokendolpher, J.C. & G.R. Camilo-Rivera. 1989. Annotated bibliography to the harvestmen of the West Indies (Arachnida: Opiliones). Occas. Pap. Florida State Coll. Arthropods, 5:1–20.

Cokendolpher, J.C. & G.O. Poinar, Jr. 1992. Tertiary harvestmen from Dominican Republic amber (Arachnida: Opiliones: Phalangodidae). Bull. British Arachnol. Soc., 9:53–56.

Eberle, W., W. Hirdes, R. Muff & M. Pelaez. 1980. The geology of the Cordillera Septentrional. Pp. 619–632, *In* Proc. 9th Caribbean Geol. Conf., August 1980, Santo Domingo.

González-Sponga, M.A. 1987. Aracnidos de Venezuela. Opiliones Laniatores I. Familias Phalangodidae y Agoristenidae. Biblio. Acad. Cien. Físic. Matemát. Nat., Caracas, 23:1–562.

Goodnight, C.L. & M.L. Goodnight. 1983. Opiliones of the family Phalangodidae found in Costa Rica. J. Arachnol., 11:201–242.

Iturralde-Vincent, M.A. & R.D.E. MacPhee. 1996. Age and paleogeographical origin of Dominican amber. Science, 273:1850–1852.

Kury, A.B. 1993. Análise filogenética de Gonyleptoidea (Arachnida, Opiliones, Laniatores). Dissertação de Doutorado, Instituto de Biociências da Universidade de São Paulo, Brasil. viii + 74 pp.

Martens, J. 1986. Die Grossgliederung der Opiliones und die Evolution der Ordnung (Arachnida). Actas X Congr. Int. Aracnol. Jaca, España, I:289–310.

Muchmore, W.B. 1993. List of terrestrial invertebrates of St. John, U.S. Virgin Islands (exclusive of Acarina and Insecta), with some records of freshwater species. Caribbean J. Sci., 29:30–38.

Schlee, D. 1990. Das Bernstein-Kabinett. Stuttgarter Beitr. Naturk., Ser. C., No. 28, pp. 1–100.

Šilhavý, V. 1979. New American representatives of the subfamily Samoinae (Opiliones, Phalangodidae, Arach.). Annot. Zool. Bot., Bratislava, no. 130, 27 pp.

Sørensen, W. 1932. Descriptiones Laniatorum (Arachnidorum Opilionum subordinis). Opus posthumum recognovit et edidit Kai L. Henriksen. K. dansk. Vidensk. Selsk. Skr. (Sec. Sci., 9 sér.), 3: 197–442.

Staręga, W. 1989. Harvestmen (Opiliones) from the Mascarene Islands and resurrection of the family Zalmoxidae. Ann. Natal Mus., 30:1–8.

Staręga, W. 1992. An annotated check-list of Afrotropical harvestmen, excluding the Phalangiidae (Opiliones). Ann. Natal Mus., 33:271–336.

DESCRIPTION OF THREE NEW SPECIES OF *NEONELLA* (ARANEAE, SALTICIDAE)

María Elena Galiano: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia". Av. Angel Gallardo 470, 1405 Buenos Aires, Argentina

ABSTRACT. Three new species of *Neonella* Gertsch 1936 are described: *Neonella mayaguez* from Puerto Rico, *Neonella colalao* and *Neonella cabana* from Argentina. The female of *Neonella antillana* Galiano 1988 is described for the first time.

RESUMEN. Se describen tres nuevas especies de *Neonella* Gertsch 1936: *Neonella mayaguez* de Puerto Rico, *Neonella colalao* y *Neonella cabana* de Argentina. La hembra de *N. antillana* Galiano 1988 se describe por primera vez.

The genera *Neon* Simon 1876, *Darwinneon* Cutler 1971 and *Neonella* Gertsch 1936 include the smallest salticids known. The biggest females reach only 2 mm in body length, and the males are smaller. *Neonella* contains at present six species (Gertsch 1936; Galiano 1965, 1988), two of them described from only one sex: *N. antillana* Galiano 1988 and *N. montana* Galiano 1988. In the present paper, the female of *N. antillana* is described for the first time and three new species are described: *Neonella mayaguez* new species from Puerto Rico, *Neonella colalao* new species and *Neonella cabana* new species from Argentina.

Few references to the natural history of *Neonella* species are known. When information has been given by the collectors, it is said that the specimens have been found on the ground, in leaf litter, and under bark or rocks. Of all spiders the most poorly known are probably those which occur in leaf litter, moss and similar surface habitats in tropical and subtropical areas. The limited data about this fauna justified the description of new species based on unique specimens. *Neonella colalao* and *N. cabana* are distinguished from the other species by the tegular pectinate process and by the presence of a male palpal patellar apophysis. However, there are other characters such as body shape, color pattern, cheliceral teeth and leg spination that would place these species within *Neonella*. They may eventually be moved to another genus when the females are studied.

METHODS

The format of the descriptions follows Galiano (1963); leg spination is described as in Platnick & Shadab (1975) with small changes. It is difficult to distinguish spines from hairs on the posterior pairs of legs, so the description is tentative. All measurements are in millimeters. *Abbreviations:* AME, ALE, PME and PLE: anterior median eyes, anterior lateral eyes, posterior median eyes and posterior lateral eyes, respectively; v = ventral, p = prolateral, r = retrolateral, ap = apical; CR = cephalic region; TR = thoracic region; MACN: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"; MCZ: Museum of Comparative Zoology, Harvard University.

Neonella antillana Galiano 1988
(Fig. 1)

Neonella antillana Galiano 1988: 444. Male holotype (MCZ) from West Indies, Jamaica, St. Andrews. Richard Reservoir, examined; Platnick 1993: 787.

Diagnosis.—*Neonella antillana* differs from *N. vinnula* Gertsch 1936 in having the copulatory openings inside pockets deeper and nearer to each other than in *vinnula*, the copulatory ducts thinner than in this species and divergent, and the spermathecae spherical, contiguous.

Description.—*Female:* Body length 1.77. Carapace length 0.73, width 0.55, height 0.24. Ocular quadrangle length 0.37, first row width 0.57, third row width 0.58. Distances ALE-PME 0.09, PME-PLE 0.05. Eye diameters:

AME 0.17, ALE 0.13, PLE 0.11. Leg spination: Tibiae I v 2-2, II v 1r-1r, III v 1p. Metatarsi I v 2-2, II v 1r-2, III 3ap; IV 1r ap. Epigynum: Fig. 1. Color: carapace light brown, with narrow dark brown marginal band. Clypeus dark brown. CR dark brown; TR with a yellow median longitudinal band with a blackish narrow band on each border. Abdomen with two dark brown dorsal longitudinal bands and a yellow longitudinal median band between them. Legs yellowish-brown with dark brown patches on distal parts of femora, patellae, tibiae and metatarsi. Palps blackish-brown, with yellow tarsi and dorsal patellae and tibiae light brown.

Material examined.—WEST INDIES. *JAMAICA:* Clarendon Parish, Salt River, 24 November 1963, 1♀ (A.M. Chickering)(MCZ); St. Andrews, Mona Heights, 25 November 1963, 1♂ (A.M. Chickering) (MCZ).
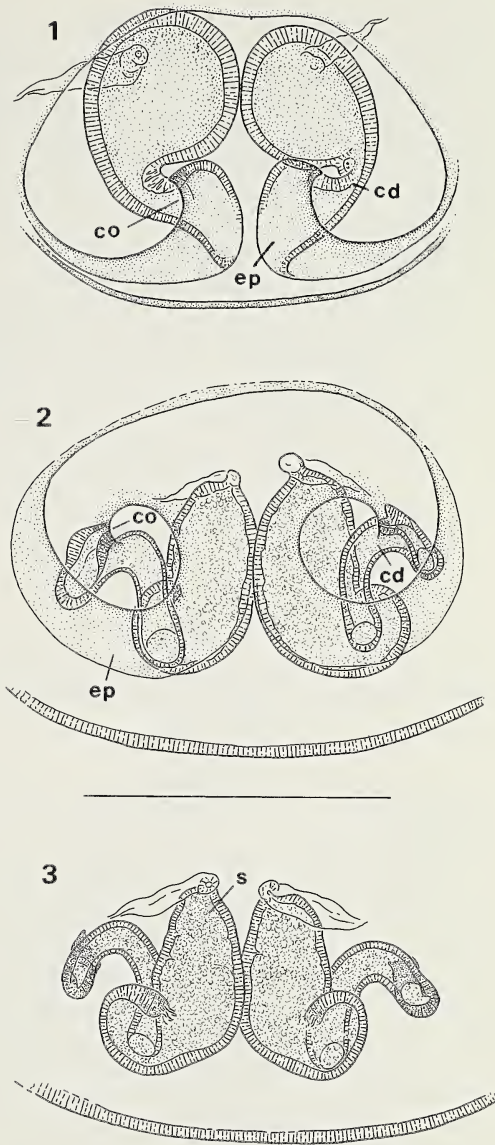

Figures 1–3.—Epigyna of species of *Neonella*. 1, *Neonella antillana*, ventral view. 2, 3. **Neonella mayaguez** new species. 2, Ventral view; 3, Dorsal view. Scale = 100 μm. (co = copulatory opening; cd = copulatory duct; ep = epigynal pocket; s = spermatheca).

Neonella mayaguez new species
(Figs. 2, 3)

Holotype.—Female from Puerto Rico. Mayagüez: University Campus, 23 January 1964 (A.M. Chickering) (MCZ).

Etymology.—A noun in apposition, after the type locality.

Diagnosis.—*Neonella mayaguez* differs from *N. vinnula* and *N. antillana* in having the copulatory openings farther from the epigastric furrow at the middle of the epigynum and external to the spermathecae.

Description.—Body length 1.67. Carapace length 0.69, width 0.52, height 0.37. Clypeus height 0.01. Ocular quadrangle length 0.32, first row width 0.53, third row width 0.52. Distances ALE-PME 0.09, PME-PLE 0.07. Eye diameters: AME 0.15, ALE 0.10, PLE 0.09. Leg spination: Tibiae I v 2-2; II v 1r-1r; III v 1r-1p. Metatarsi I, II v 2-2; III, IV 3ap. Epigynum: epigynal pockets contiguous; copulatory openings at the sides of the epigynal plate and far from the epigastric furrow (Fig. 2); spermathecae tubular, contiguous (Fig. 3). Color: carapace light brown, CR blackish with few reddish brown hairs; RT with yellow lateral marginal bands and a median longitudinal band. Abdomen blackish-brown with three yellow longitudinal bands, the median one being wider; sides and venter yellow. Legs yellow, blackish bands on prolateral sides on femora, and transversely distal on patellae and tibiae. Palps yellow, lateral sides blackish.

Material examined.—Only the holotype.

Neonella cabana new species
(Figs. 4–6, 11, 12)

Holotype.—Male from Argentina, Córdoba Province: Cabana, July 1950 (M. Birabén) (# 9557 MACN).
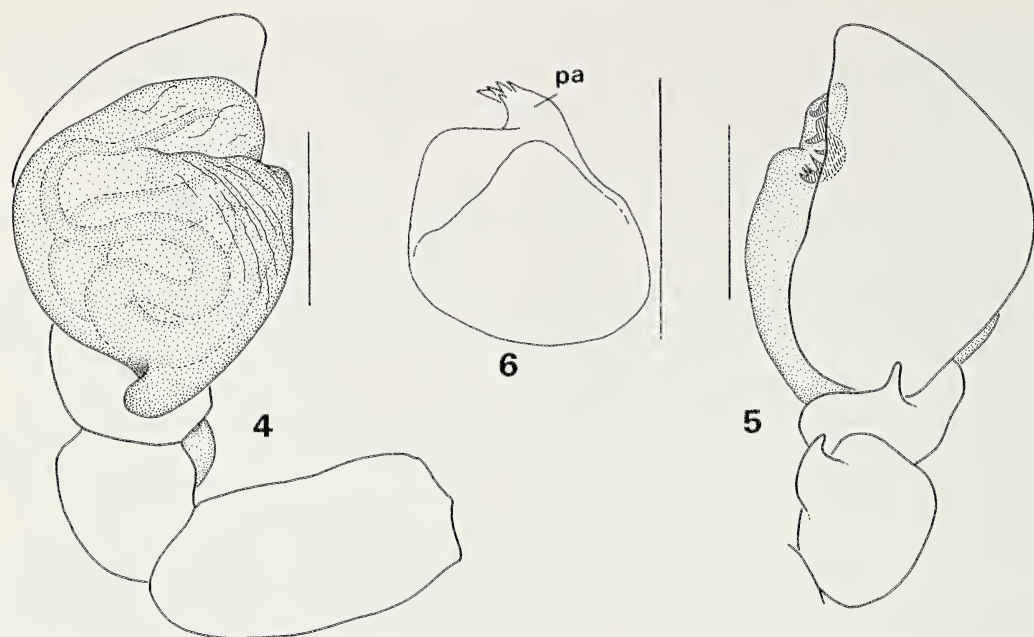
Figures 4–6.—Left palp of *Neonella cabana* new species. 4, Ventral view; 5, Retrolateral view; 6, Patella, prolateral view showing internal face of patellar apophysis. Scales = 100 μm. (pa = patellar apophysis).

Etymology.—A noun in apposition, after the type locality.

Diagnosis.—*Neonella cabana* and *N. colalao* new species can be distinguished from all the other species of the genus by the pectinate process on the apical division of the tegulum and by the presence of a retrolateral apophysis on palpal patella. *Neonella cabana* differs from *N. colalao* by the blunt embolic apex (no terminal rami), by the almost spherical tegular apical division and by thinner and apparently more numerous teeth of the pectinate process.

Description.—Carapace length 0.70, width 0.49, height 0.31. Clypeus height 0.02. Ocular quadrangle length 0.31, first row width 0.51, third row width 0.50. Distances: ALE-PME 0.07, PME-PLE 0.04. Eye diameters: AME 0.15, ALE 0.11, PLE 0.10. Leg spination: Tibiae I v 2-1r; II v 1r-1r; III, IV v 1p. Metatarsi I, II v 2-2; III, IV 3ap. Palp: (Figs. 4–6, 11, 12). Patellar apophysis with small acute teeth on the internal side; tibial apophysis with parallel sides, a little longer than in *N. colalao*. Apical division of the tegulum spheroidal; embolus lamellar, a little curved, distal end blunt with the terminal opening of the seminal duct in the border. Pectinate process with a wide base and about ten long and sharp teeth. Color: carapace light brown; CR blackish with few brown hairs regularly distributed; TR with a median longitudinal yellow band. Clypeus blackish. Abdomen with bright reddish-yellow dorsal scutum with few brown hairs; a dense tuft of white plumose hairs at the apical end, covering the anal tubercle; sides of the abdomen yellow, with brown hairs more dense than the dorsal. Epigastric area sclerotized; no ventral scutum. Legs yellowish-brown, with blackish bands on sides of femora and tibiae I and II.

Material examined.—Only the holotype.

Note.—*Neonella cabana* might be *N. montana* Galiano 1988, which was described after a female whose epigynum has small differences from the typical *Neonella*.

Neonella colalao new species
(Figs. 7–10)

Holotype.—Male from Argentina, Tucumán Province: San Pedro de Colalao (4 km W road to Hualinchay), November 1994 (M. J. Ramírez) (# 9556 MACN).

Etymology.—A noun in apposition, after the type locality.

Diagnosis.—*Neonella colalao* differs from
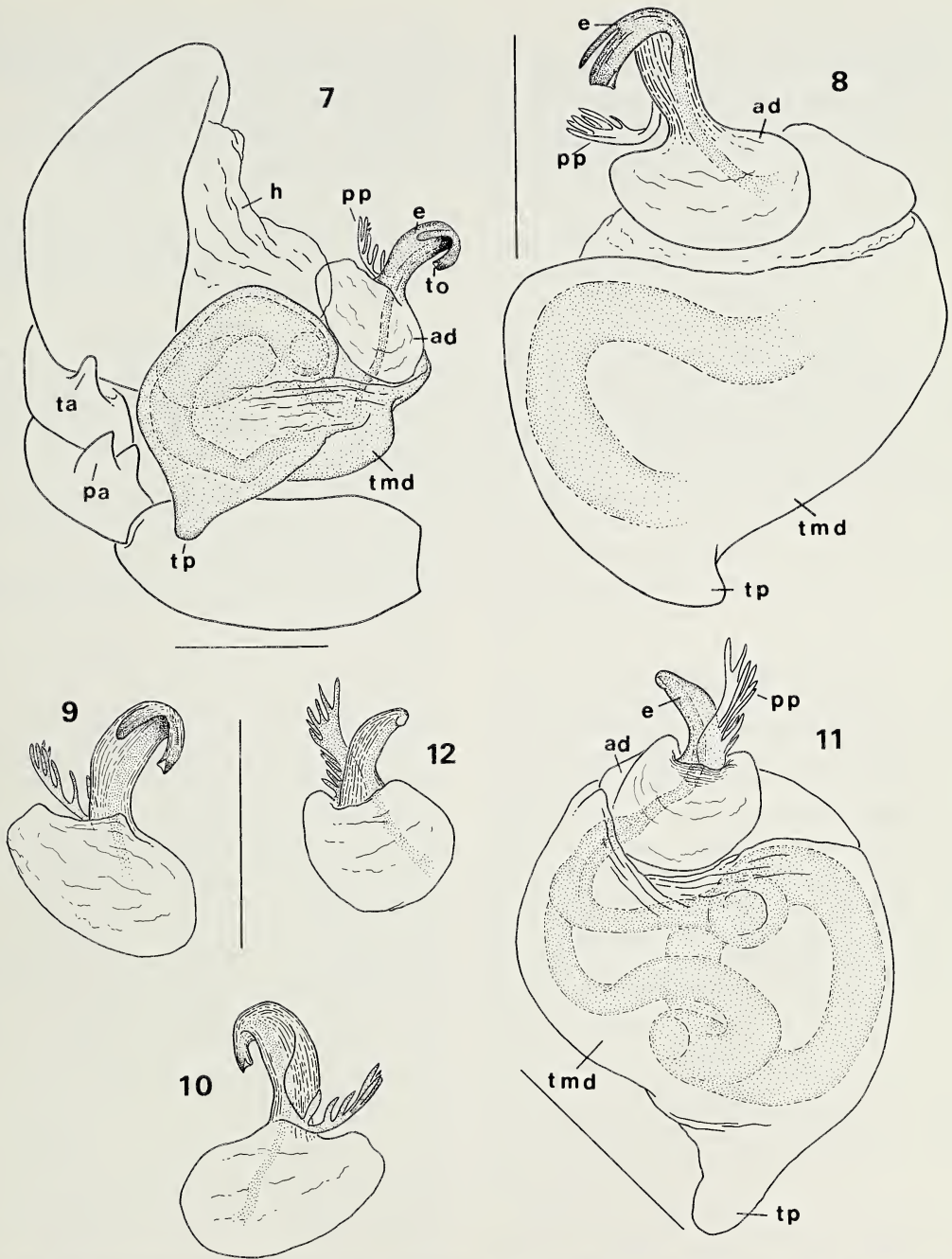
Figures 7–12.—Palps of species of *Neonella*. 7–10, **Neonella colalao** new species. 7, Retrolateral view of the right palp with expanded bulb. 8, Bulb, ventral view; 9, Apical division, retroventral view; 10, Dorsal view. 11, 12, **Neonella cabana** new species. 11, Ventral view of the left bulb; 12, Apical division, dorsal view. Scales = 100 μm. (ad = tegular apical division; e = embolus; h = hematodocha; pa = patellar apophysis; pp = pectinate process; ta = tibial apophysis; tmd = tegular median division; to = terminal opening of the sperm duct; tp = tegular process).

N. cabana by having two terminal rami on the embolus.

Description.—Body length 1.60. Carapace length 0.71, width 0.52, height 0.31. Clypeus height 0.02. Ocular quadrangle length 0.34; first row width 0.53, third row width 0.54. Distances: ALE-PME 0.07, PME-PLE 0.05. Eye diameters: AME 0.18, ALE 0.12, PLE 0.11. Leg spination: Tibiae III v 1p. Metatarsi I v 1r-1r; II v 2 ap; III, IV 2ap. Palp: (Figs.7–10). A conical retrolateral apophysis on patella, with several denticles on its inner face; retrolateral tibial apophysis short. Tegular median division with a conical process that covers the ventral side of tibia; apical division as a transverse membranous ovoid from whose distal and dorsal side (that touches the cymbium) arises the embolus. Embolus lamellar, a little curved, with two subequal apical rami that curve to the base. On the tip of the prolateral ramus is the terminal opening of the sperm duct. Near the base of the embolus but arising from the apical division is a pectinate process. Color: carapace yellow, narrow black marginal band, wider yellow submarginal band; CR blackish, TR blackish on the anterior half and with blackish spots on the thoracic slope at the sides of a median yellow band. Clypeus dark brown. Abdomen yellow with blackish dispersed spots; dorsal scutum bright yellow; sides yellow; at the dorsal end of the abdomen, covering the anal tubercle, a dense tuft of white plumose hairs. Both sides of pedicel black. Venter yellow, with two black lateral bands; a black ring around the base of the spinnerets. Epigastric area sclerotized, no ventral scutum. Legs translucent, yellow, with distal dorsal blackish bands on patellae, tibiae and metatarsi.

Material examined.—Only the holotype.

LITERATURE CITED

Galiano, M.E. 1963. Las especies americanas de arañas de la familia Salticidae descriptas por Eugène Simon. Redescripciones basadas en los ejemplares típicos. Physis (Buenos Aires), 23(66):273–470.

Galiano, M.E. 1965. Descripción de *Neonella minuta* n. sp. (Araneae, Salticidae). Revta Soc. Entomol. Argentina, 27(1–4):25–28.

Galiano, M.E. 1988. New species of *Neonella* Gertsch, 1936. (Araneae, Salticidae). Rev. Suisse Zool., 95(2):439–448.

Gertsch, W.J. 1936. Further diagnoses of New American spiders. American Mus. Novit., 852: 1–27.

Platnick, N.I. 1993. Advances in spiders taxonomy 1988–1991 with new synonymies and transfers 1940–1980. New York Entomol. Soc. American Mus. Nat. Hist., New York.

Platnick, N.I. & M.U. Shadab. 1975. A revision of the genus *Gnaphosa* (Araneae, Gnaphosidae) in America. Bull. American Mus. Nat. Hist., 155(1):1–66.

NOTES ON THE NEOTROPICAL SPIDER GENUS *MODISIMUS* (PHOLCIDAE, ARANEAE), WITH DESCRIPTIONS OF THIRTEEN NEW SPECIES FROM COSTA RICA AND NEIGHBORING COUNTRIES

Bernhard A. Huber[1]: Escuela de Biología, Universidad de Costa Rica, Ciudad Universitaria, Costa Rica

ABSTRACT. Notes on the morphology and natural history of Central American *Modisimus* species are given. Thirteen new species from Costa Rica, Panama and Nicaragua are described. This highlights the greatly underestimated diversity of the genus in the region (only one species has previously been recorded from Costa Rica). New names are: *Modisimus bribri* new species, *M. cahuita* new species, *M. caldera* new species, *M. coco* new species, *M. dominical* new species, *M. guatuso* new species, *M. madreselva* new species, *M. nicaraguensis* new species, *M. pittier* new species, *M. sanvito* new species, *M. sarapiqui* new species, *M. selvanegra* new species and *M. tortuguero* new species. Seven further species of the genus are redescribed in order to ascertain their distinctiveness from the new species: *M. dilutus* Gertsch 1941 and *M. pulchellus* Banks 1929 from Panama, *M. inornatus* Cambridge 1895, *M. maculatipes* Cambridge 1895, *M. putus* Cambridge 1895 (which is newly synonymized with *M. maculatipes*), *M. propinquus* Cambridge 1896 from Mexico and *M. texanus* Banks 1906 from Texas.

The genus *Modisimus* was established by Simon (1893b) for a single species from the Dominican Republic (*M. glaucus* Simon 1893). Presently it contains some 45 species, mostly from Central America and the West Indies. Only one species has been reported from the USA (*M. texanus* Banks 1906), while all of the five South American species may be either misplaced, introduced, or erroneously assigned to South America (Huber in press b). Thus, the genus appears to be restricted to Central America and the West Indies, but the pholcid faunas of Colombia and other northern South American countries are almost unknown and may well include representatives of *Modisimus*.

The genus is weakly defined by the presence of a prominent eye turret, an elevation of the prosoma that carries the eyes. *Modisimus* is apparently part of a group of genera that share the geographic distribution (North and Central America and the West Indies) and the presence of a pointed and upward projecting apophysis on the male pedipalpal femur ("*Modisimus* group" - Huber in press b). This group includes also the genera *Anopsicus*

Chamberlin & Ivie 1938, *Psilochorus* Simon 1893, *Bryantina* Brignoli 1985, and some species currently misplaced in the genera *Coryssocnemis* Simon 1893 and *Blechroscelis* Simon 1893. The genus *Hedypsilus* Simon 1893 has been discussed recently (Huber 1996) and no character was found that would distinguish it from *Modisimus*. It was therefore synonymized with *Modisimus* and includes "short-legged" *Modisimus*. *Anopsicus* and *Psilochorus* are also "short-legged", but their eye-regions are hardly elevated, and *Psilochorus* has well developed anterior median eyes (which are missing or reduced to vestiges in *Modisimus*). *Bryantina* might be a synonym of *Modisimus*. Only further study can clarify the phylogenetic relationships within the "*Modisimus* group".

The most recent published checklist of Costa Rican spiders (Zuñiga 1980) includes only one representative of the pholcid genus *Modisimus*: *M. inornatus* Cambridge 1895. This species was originally described from Mexico and was later recorded from Panama (Petrunkevitch 1925) and Costa Rica (Reimoser 1939), but the existing descriptions (Cambridge 1895, 1896, 1899; F. Cambridge 1902) are not sufficient for the great biodiversity we encounter, casting doubt on the identifications

[1]Current address: Dept. of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024 USA.

of later authors. The primary incentive for the present study was the contrast between this single doubtful record and the considerable number of unidentified species in collections. Thus, the focus of this paper is on the diversity of the genus in a comparatively small geographic region, rather than on a clade or a distinctive species group. Although the emphasis is on Costa Rican representatives, some previously described Mexican and Panamanian *Modisimus* species were studied and are redescribed in order to avoid the creation of junior synonyms, because the existing descriptions did not allow their separation from Costa Rican specimens (*M. inornatus*, *M. dilutus*, *M. pulchellus*, *M. texanus*). Moreover, three species originally described from Mexico (*M. maculatipes*, *M. putus*, *M. propinquus*) have also been recorded from Panama (Banks 1929; Nentwig 1993; Chickering 1936), suggesting their occurrence in Costa Rica. It turns out that none of these species has been collected in Costa Rica, and the Panamanian records are probably based on misidentifications. Apart from this, three species from neighboring countries (Panama, Nicaragua) are also newly described. "Short legged" *Modisimus* (= "Hedypsilus", synonymized by Huber 1996) are excluded because they were recently treated elsewhere (Huber 1996—only one species is known from Costa Rica: *M. culicinus* Simon 1893).

METHODS

This study is primarily based on the collections of the Instituto de Biodiversidad, Costa Rica (INBIO), the Escuela de Biología of the Universidad de Costa Rica (UCR), and the author's collection (the latter will eventually be incorporated into the UCR collection). Unless otherwise noted, the material studied is in the author's collection. Types were borrowed from the following institutions: Museum of Comparative Zoology, Cambridge (MCZ), American Museum of Natural History, New York (AMNH), Natural History Museum, London (BMNH), Senckenbergmuseum Frankfurt (SMF), Muséum National d'Histoire Naturelle, Paris (MNHN). In addition to the types of all the species treated in the present paper, I have seen the following: *M. cornutus* Kraus 1955, *M. culicinus* Simon 1893, *M. glaucus* Simon 1893, *M. globosus* Schmidt 1956, *M. palenque* Gertsch 1977. The pub-

lished descriptions of species whose types were not studied were considered sufficient to separate those species from the newly described species.

Descriptions follow the style currently used for pholcid spiders, with the following exceptions: while much emphasis has traditionally been on the pattern of eyes (relative size and position, curvature of eye rows, etc.), this character is of very limited value in closely related species and is usually described only by means of a figure. In contrast, more emphasis is laid on the genitalia, especially the male paracymbium or "procursus", and the male chelicerae that are sexually modified. Drawings of the entire palps are usually accompanied by drawings of details (femur apophysis, bulb, procursus) since small changes in the angle of view may drastically change their shape. The same problem applies to the prosoma (compare Figs. 1 and 2).

Drawings were made with a compound microscope with camera lucida and later completed with a dissecting microscope. Measurements (all in mm) were taken with ocular micrometers in a compound or a dissecting microscope. Averages (arithmetic means) are given for $n \geq 5$. Prosoma length was defined as the distance between frontal face of eye region and posterior border of carapace medially, but it varies widely with the angle at which the prosoma is viewed (it is hardly possible to position the spider in a standard angle unless all the legs are cut off). "Carapace" is referred to as the dorsal part of the prosoma. The most accurate indicators of size are probably prosoma width and tibia length. Total size is simply the sum of prosoma length and opisthosoma length, regardless of the petiolus, and is given as an approximate indication of overall size. For reasons of space, measurements for all segments (except coxa and trochanter) are given only for leg 1. For other legs, only total length is given. The tibia index ("tibind") is the length of the tibia divided by its width at the middle, and is thus a measure of the "slenderness" of the legs. In the diagnoses, species with an average total length of > 3 mm are defined as "large", those smaller that 2.5 mm are "small".

Morphological details (spinnerets, male genital pore, hair structure) were studied with a Hitachi S-570 scanning electron microscope.

Modisimus Simon 1893

Modisimus Simon 1983b: 484–485, figs. 480–482, 485. Type species: *Modisimus glaucus* Simon 1893, in MNHN, examined. Simon 1893a: 322. Gertsch 1971: 66. Brignoli 1973: 219–221. Gertsch & Peck 1992: 1192–1193. Huber 1996: 238–239.

Modisimops Mello-Leitão 1946: 50. Type species: *M. dilutus* Gertsch 1941, in AMNH, examined. Synonymized with *Modisimus* by Brignoli 1973, with *Hedypsilus* by Gertsch & Peck 1992.

Hedypsilus Simon 1893b: 484–486, figs. 483–484, 486. Type species: *H. culicinus* Simon 1893, in MNHN, examined. Simon 1893a: 322. Gertsch & Peck 1992: 1192. Huber 1996: 238–239. Synonymized by Huber 1996.

Diagnosis.—Small to medium sized (1.5–4 mm body length) pholcids with elevated eye region (eye turret; Figs. 46, 149, 183). Usually with six eyes, rarely with punctiform anterior median eyes (Fig. 190), with pointed and upward projecting apophysis on the male pedipalpal femur (Fig. 4). The closest relatives are: *Anopsicus* (six eyes in two triads, no eye turret), *Psilochorus* (eight eyes on weakly elevated eye region), *Bryantina* (possibly a synonym of *Modisimus*), and some probably misplaced Central American "*Coryssocnemis*" and "*Blechroscelis*" (these also lack an eye turret and have eight eyes).

Morphology.—The species treated in the present study are relatively small spiders (about 2–4 mm total length), but their long legs (the first legs of males range from about 18–45 mm each) make them fairly conspicuous. Depending on the habitat (see below) they are either dark (ochre, brown, with black spots) or light (pale ochre-yellow, greenish). The habitus of males and females differs only slightly (Figs. 64–66, 182–184), the female having a smaller prosoma and shorter legs, but often a more globular and larger opisthosoma (depending on the amount of eggs). Sexual dimorphisms occur in the chelicerae (those of the males are equipped with modified hairs) and sometimes the femora of the anterior legs (again, those of the male may be equipped with modified hairs in the form of spines). The most puzzling sexual dimorphism concerns the femora of all legs that are set with high numbers of short (about 50 μm), fine (diameter proximally about 1.5 μm, distally 0.3 μm), erect hairs in males (Fig. 18), while the legs of females have only very few hairs of

this type. These hairs remind one of chemosensitive sensilla ("taste-hairs" - Foelix & Chu-Wang 1973), but the tips are pointed rather than blunt, and it would be very unusual for taste hairs to be located in such densities on the femora while distal leg segments are equipped with much lower densities (see the tibia in Fig. 33). Scanning micrographs of the tips did not reveal any pores. Characteristically curved hairs (Fig. 33) occur on the tibiae and metatarsi of most species, usually both in males and females. They are often restricted to the anterior legs, and this trend is stronger in females than in males.

The male genitalia offer the best characters for species discrimination (Figs. 4, 5). The pedipalpal femur is ventrally equipped with a pointed, sclerotized apophysis. The cymbium bears a prominent paracymbium (in pholcids called procursus) which is usually highly species specific and often carries a dorsal spine (or "flagellum"). The bulb lacks an embolus (which is common in American pholcids - Huber unpubl. data); the sperm duct does not run through any elongated projection but opens near the basis of the bulbal apophysis that is usually set with small denticles and has often been misinterpreted as the embolus (Petrunkevitch 1929; Bryant 1940, 1948). Also the pedipalpal coxae are sexually modified in males: they bear a simple apophysis that stabilizes the palp during copulation (Huber in press b). The female genitalia are marked externally by a more or less sclerotized plate (the "epigynum") that is diagnostic in only a few species. Internally the simple copulatory chamber (uterus externus) bears dorsally a pair of pore plates that mark the position of the vulval glands, and is connected to the oviduct by a simple "valve" (Huber in press a).

While the function of the erect hairs and spines on the male femora remains to be established, some other sexually dimorphic and genitalic characters have been interpreted functionally (Huber in press b). The modified hairs on the male chelicerae contact the female epigynum during copulation and may provide the male information regarding his position towards the female, or stimulate the female. The procursi are inserted into the female copulatory chamber. The bulbal apophyses are also inserted into the female and their denticles apparently function to increase the friction between male apophysis and the ven-

tral surface of the uterus externus, but might also be involved in stimulation. The pedipalpal femur apophysis hooks into a pouch of the bulb and stabilizes the bulb during copulation.

The spinnerets of three species were studied (*M. guatuso* new species, *M. dominical* new species, *M. culicinus*) and showed little interspecific variation, but differed from *Pholcus phalangioides* (Fuesslin 1775) by having only two spigots on each anterior lateral spinneret (the "widened spigot" and the "pointed spigot" of Platnick et al. 1991; *P. phalangioides* has several "smaller widened spigots" in addition). The male genital pores of the three *Modisimus* species mentioned above lack spigots (in contrast to several other pholcid genera - Huber unpubl. data).

Natural history.—Most of the species treated herein (at least those collected by the author) live in webs whose dominant feature is a dome shaped sheet of silk. The structure of the web has been studied in one species (*M. guatuso* new species - Eberhard & Briceño 1983 under *M.* sp. C; Briceño 1985; Eberhard 1992) but details vary among species (W.G. Eberhard pers. comm.). They occupy a variety of habitats: most species were found in shady, humid places near the ground (the dark species mentioned above), with their webs extended between buttresses of trees, fallen logs, or rocks. A few were found under fallen leaves, in correspondingly tiny webs, while others build their webs higher up in the vegetation (the light species), usually with at least one part of the domed sheet in connection with the underside of a leaf. Most species have only been found in humid forests. Adult males and females occur at any season, but population density may fluctuate significantly (Huber unpubl. data). The spiders are active during the day (several pairs of *M. guatuso* new species were found in copula around noon); their night activities are unknown (*cf.* nocturnal pholcids in Indo-Australian rainforests - Deeleman-Reinhold 1986).

Some aspects of the reproductive biology have been studied in *M. guatuso* new species (Eberhard & Briceño 1983, 1985 under *M.* sp. C; Huber unpubl. data). Males and females of several species were often found together in one web. In a monthly survey of a *M. guatuso* new species population (Reserva Biol. Leonel Oviedo, Univ. de Costa Rica) over 21 months, I recorded 345 pairs, 296 single females, and 171 single males (*cf.* similar results in Eberhard & Briceño 1983). This is probably an underestimate of pairs, since the spiders often hide when the nearby vegetation is moved so that I may have overlooked one of the two partners. Males "guard" only females without egg-sacs or spiderlings: in only 2 out of 345 pairs the female was carrying an egg-sac, and in one there were also spiderlings in the same dome. Males were found to be dominant over females, but to be "chivalrous" by frequently ceding prey to the guarded female (Eberhard & Briceño 1983 - their study is based on the same population).

The general pattern of courtship and copulation closely resembles that found in other pholcids (Huber 1994; Uhl et al. 1995; Huber & Eberhard 1997; Huber 1996, 1997, in press b). Of 13 *M. guatuso* new species copulations observed in the laboratory, three started with "flubs", i.e., unsuccessful attempts to couple (two "flubs" each). The spiders copulated in Helversen's (1976) "position of web spiders", the male palps were rotated 180° before copulation, and the genitalia were inserted symmetrically and simultaneously into the female copulatory chamber. Copulations lasted 13.1 min, 14.9 min, 15.8 min and 21.2 min in four pairs with virgin females (the other pairs were freeze-fixed between 2–12 min after coupling). During copulation males performed rhythmic movements with their palps, legs and abdomens. The palps were moved in a lateral direction, and the frequency of this movement slowly decreased from about one movement every 2 sec at the beginning to about one movement every 10 sec at the end of copulation. The movements of right and left palp were asynchronous, with one palp being slightly ahead. The order of first and second palp to move alternated strictly between right and left side. One obvious result of the palpal movements was a rhythmic lateral movement of the female abdomen. Both males and females tapped their partners with the anterior legs during copulation, but usually only during the first minutes. Short bursts of male abdomen vibration accompanied the palpal movements. During the first minutes of copulation the male spinnerets consistently touched the female abdomen, usually anterior to her spinnerets. This caused the male abdomen to move in the same direction, amplitude and frequency as the female abdomen.

No thread was secreted from the male spinnerets.

Many females collected in the field had a "copulatory plug", i.e., a more or less hard globular mass protruding from the copulatory chamber. In a survey of 145 females from 7 species, 59 females (41%) had a plug. This is probably an underestimate of plugged females for three reasons: (1) females lose the plug when laying eggs (confirmed in two cases in *M. guatuso* new species), and 14 of the females without plug had been kept in the laboratory for some time before fixing them and may have laid eggs; (2) in 7 other females without plugs, the epigynum was erected and the uterus externus wide open, suggesting that a plug had been removed (e.g., to study the epigynum); (3) in the field I tended to collect females with egg-sacs in order to be sure to get adults, thus perhaps producing a bias towards unplugged females. In one female (*M. cahuita* new species) the plugged genitalia were serially sectioned, and the protruding mass was simply an extension of the mass inside the uterus externus, consisting of the same mixture of sperm and matrix that is usually found in pholcid genitalia (Uhl 1994). It is worth noting that plugs may repeatedly have been misinterpreted, either as parts of the female genitalia (Cambridge 1895) or as protruding eggs (Petrunkevitch 1929).

As in other studied pholcids (Uhl 1993; Huber in press a, in press b) *Modisimus* females can produce several successive fertile egg-sacs without remating, indicating the ability of storing sperm without having seminal receptacles. Females of *M. guatuso* new species produced up to three fertile egg-sacs in captivity, those of *M. selvanegra* new species up to four. The average number of hatched spiderlings per egg-sac was 13 in *M. guatuso* (22 egg-sacs, range 5–27), 9 in *M. selvanegra* (24 egg-sacs, range 2–17). After producing these fertile egg-sacs, most females continued laying eggs, but no spiderlings emerged from these. Sperm depletion and lab conditions (spiders were only fed *Drosophila* flies) may both be accountable for this observation.

Modisimus bribri new species
(Figs. 1–23)

Type data.—Male holotype and female paratype from forest at sea level on Bocas del Toro Island, Bocas del Toro Province, Panama, 23 April 1995 (B.A. Huber) (UCR).

Etymology.—Named for the Bribri, an indigenous Costa Rican people.

Diagnosis.—Light species (pale greenish-yellow) without black spots on opisthosoma (Figs. 1–3), otherwise morphologically similar to *M. guatuso*, and equally variable. Distinguished from light relatives by procursus with long and slender dorsal spine (Figs. 6–8; *M. madreselva* and *M. sanvito* have short dorsal spines: Figs. 95, 122; *M. coco* has a stout dorsal spine: Fig. 50).

Description.—*Male holotype:* Carapace pale ochre-yellow, with darker median stripe, clypeus white without darker markings, chelicerae and pedipalps pale ochre-yellow, sternum pale orange. Legs ochre-yellow with darker rings at femora (distally) and tibiae (proximally and distally). Distal rings on femora and tibiae followed by light rings. Opisthosoma dorsally bluish-green, with characteristic pattern of white spots dorsally (Fig. 1; these often disappear in alcohol), without black spots; ventrally lighter, only genital plate brownish. Six eyes on eye turret, pedipalps as shown in Figs. 4–5, procursus, bulb and femur apophysis as shown in Figs. 6, 9–10, 13, chelicerae with one patch of modified hairs on each side (Fig. 16). Femora 1 and 2 with a row of spines ventrally (Fig. 18). *Measurements:* Total length: 2.8, prosoma length: 0.9, width: 0.9, opisthosoma length: 1.9; leg 1: fem: 7.7, pat: 0.4, tib: 7.5, met: 14.2, tar: 2.2, total: 32.0, tibind: 79; leg 2: 20.5, leg 3: 14.8, leg 4: 18.0.

Female paratype: Colors mostly as in male, sternum not orange but pale brownish-ochre. Epigynum as shown in Fig. 19, brown. Legs without spines. *Measurements:* Total length: 2.4, prosoma length: 0.8, width: 0.8, opisthosoma length: 1.6; leg 1: fem: 5.0, pat: 0.3, tib: 4.9, met: 8.8, tar: 1.6, total: 20.6, tibind: 62; leg 2: 12.8, leg 3: 9.2, leg 4: 12.0.

Variation.—As in *M. guatuso* new species there is considerable inter-population variation, whereas variation within populations is usually small. The lack of correlated variation between varying characters and the presence of intermediate forms led to lumping of several populations into one highly variable species. Some populations are included with hesitation (especially from the Costa Rican Pacific slope and Cordillera Central). Only
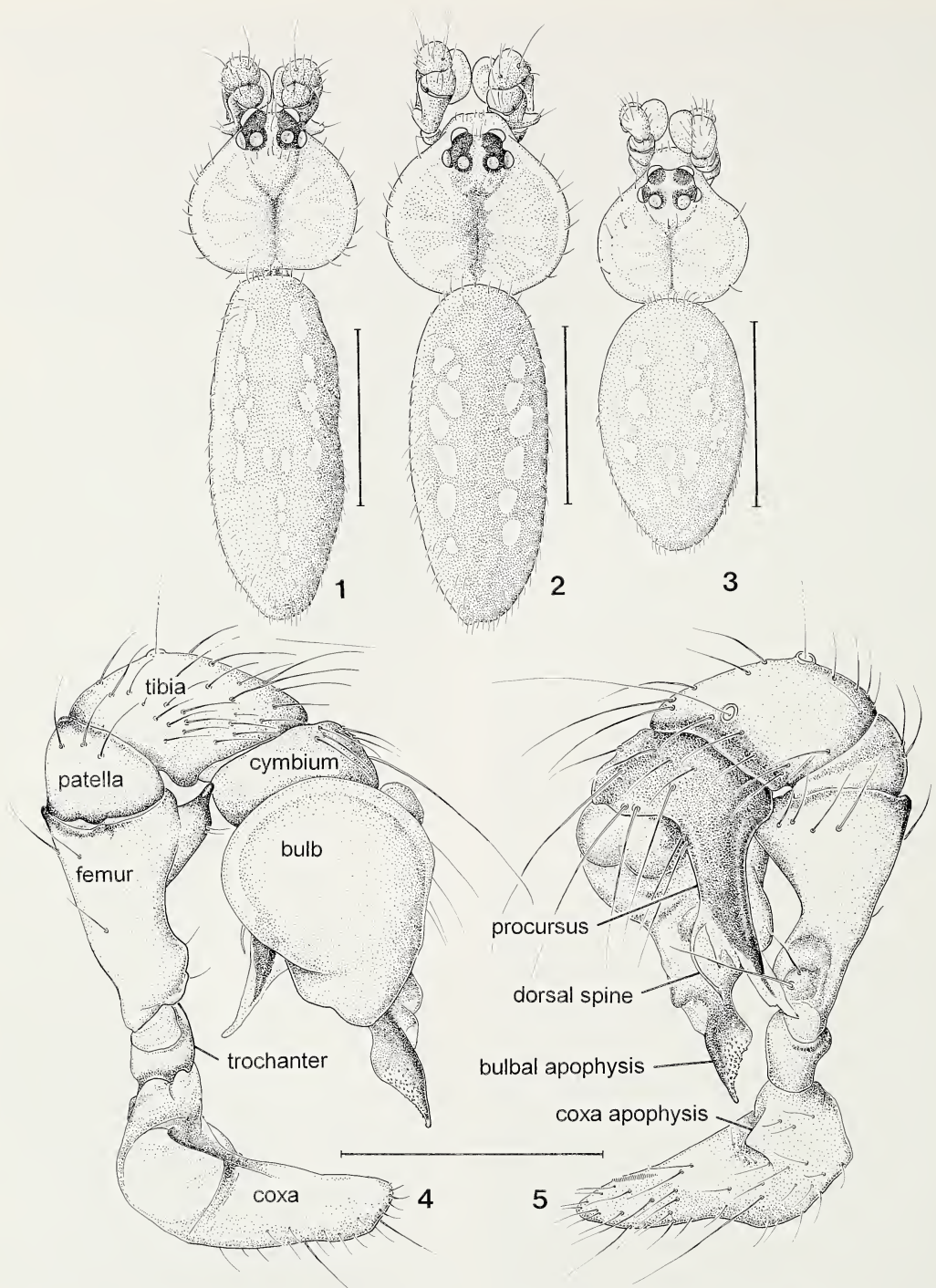
Figures 1–5.—***Modisimus bribri*** new species. 1–3. Males in dorsal view; note the differences in the shape of the prosoma due to slight differences in the angle of view. 1, Bocas del Toro (type locality); 2, Zurquí; 3, La Gamba; 4, Left male pedipalp, slightly extended, bulb rotated, prolateral view; 5, Left male pedipalp, slightly extended, bulb rotated, retrolateral view. Scale bars = 1 mm (1–3); 0.3 mm (4–5).
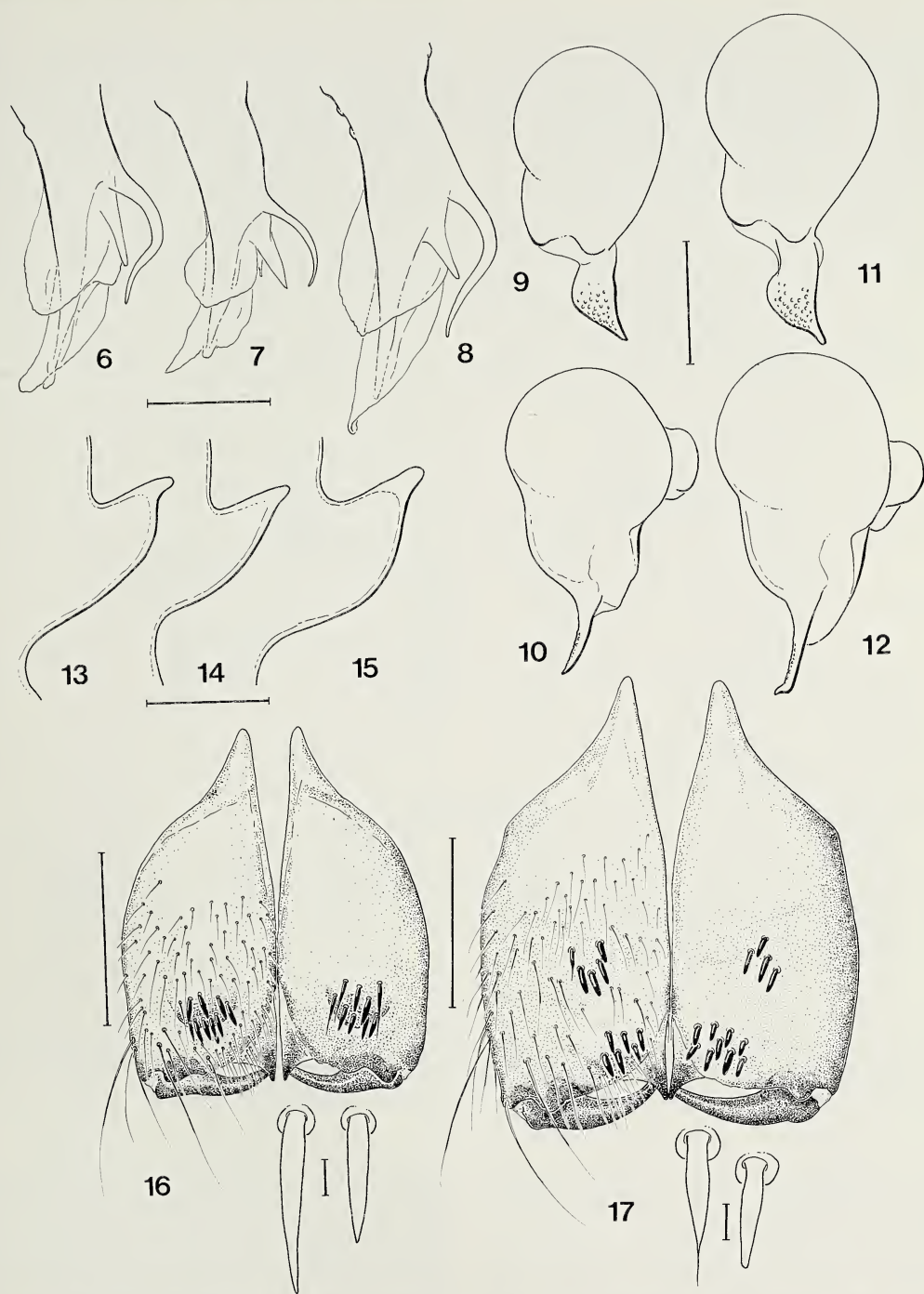
Figures 6–17.—***Modisimus bribri*** new species. 6, Left procursus, prolateral view, Bocas del Toro (type locality); 7, Left procursus, prolateral view, Bajo La Hondura; 8, Left procursus, prolateral view, San Ramón; 9, Left genital bulb, ventral view, Bocas del Toro (type locality); 10, Left genital bulb, prolateral view, Bocas del Toro (type locality); 11, Left genital bulb, prolateral view, San Ramón; 12, Left genital bulb, prolateral view, San Ramón; 13–15, Male palpal femur apophysis. 13, Bocas del Toro (type locality); 14, Bajo La Hondura; 15, Zurquí; 16, 17, Male chelicerae, frontal view, with two modified hairs enlarged. 16, Bocas del Toro (type locality); 17, Zurquí. Scale bars = 0.1 mm (6–8, 13–15); 0.2 mm (9–12, 16–17); 0.01 mm (modified hairs).
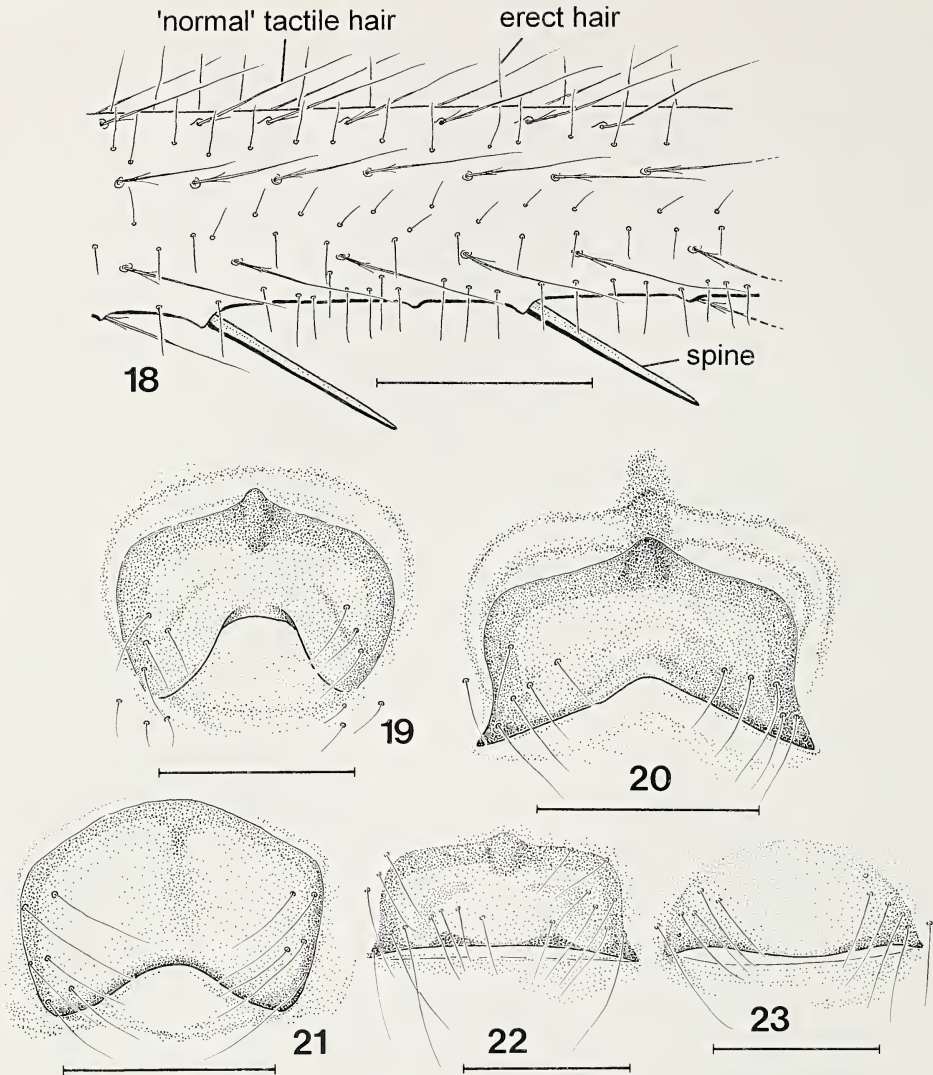
Figures 18–23.—*Modisimus bribri* new species. 18, Right femur 1 in retrolateral view, showing spines 11 and 12 out of 20, male from La Selva; 19–23, Epigyna in ventral view. 19, Bocas del Toro (type locality); 20, Cahuita; 21, Zurquí; 22, San Ramón; 23, Uvita. Scale bars = 0.2 mm.

statistical analyses on larger samples and/or biological experiments may eventually justify or reject the present limitation.

Size variation is considerable, though not as extreme as in *M. guatuso* new species. The most common pattern on the opisthosoma is that shown in Figs. 1, 3. A different pattern is shown in Fig. 2. The shape of the opisthosoma is usually elongate (Figs. 1, 2), but can be oval (Fig. 3), especially in smaller individuals. The male femur 1 is usually set with a row of up to about 20 spines; in several populations, however, there are also males without spines

on their femora (Zurquí, Bajo la Hondura, Hitoy Cerere). The male chelicerae are provided with either one or two patches of spines on each side (Figs. 16, 17), or with an intermediate pattern. The spines are never characteristically shaped (as in some other species, Figs. 43, 59, 117).

The male genitalia are strikingly similar to those of *M. guatuso* new species, and show much the same range of variation. The procursus varies both in size and shape (Figs. 6–8). However, some of the variation shown may be artificial, as most of the distal struc-

tures on the procursus are membranous. Apart from variation in size, the bulb shows little variation (Figs. 9–12). However, the bulb of several other species is very similar (Figs. 75–80, 144–145), which renders the bulb of little diagnostic value. The pedipalpal femur apophysis varies as shown in Figs. 13–15. The epigynum never shows any protrusions, but is a simple, though highly variable, sclerotized plate (Figs. 19–23).

Tibia 1 in other material: Bocas del Toro: 7♂: 6.4–8.3 (x̄ = 7.5), 12♀: 4.3–5.4 (x̄ = 4.8). Cahuita: 5♂: 7.4–8.9 (x̄ = 8.3), 6♀: 4.9–5.3 (x̄ = 5.2). Hitoy Cerere: 3♂: 8.3, 8.6, 9.3; 2♀: 5.5, 6.2. San Miguel: 1♂: 9.3. Tortuguero: 7♂: 8.2–9.0 (x̄ = 8.5); 17♀: 5.1–5.9 (x̄ = 5.5). Cariari: 1♀: 5.4. Finca La Selva: 16♂: 7.5–9.6 (x̄ = 8.4), 7♀: 5.2–5.7 (x̄ = 5.4). Puerto Viejo: 1♂: 9.0. Estacion Barva: 1♂: 6.5; 2♀: 4.6, 4.9. Zurquí: 10♂: 7.0–8.3 (x̄ = 7.7), 9♀: 5.2–5.8 (x̄ = 5.4). Bajo la Hondura: 7♂: 6.5–7.8 (x̄ = 7.1), 2♀: both 4.8. Quebrada González: 5♂: 7.5–8.6 (x̄ = 8.3), 1♀: 6.0. San Ramón: 8♂: 7.1–8.7 (x̄ = 7.9), 6♀: 4.9–5.7 (x̄ = 5.3). Tilarán: 8♂: 8.1–9.1 (x̄ = 8.6), 7♀: 4.6–5.5 (x̄ = 5.1). El Cedral: 1♀: 4.9. Uvita: 3♂: 6.4, 7.1, 7.2; 2♀: 4.1, 4.7. La Gamba: 5♂: 6.4–7.5 (x̄ = 7.0); 3♀: 4.2, 4.3, 4.5.

Other material examined.—PANAMA: 10♂13♀ from type locality (same collection data as types). COSTA RICA: *Prov. Limón:* Cahuita, 500 m S of village, sea level, 7♂6♀, 13–14 June 1995 (B.A. Huber). Hitoy Cerere Biol. Station, elev. 150–200 m, 3♂2♀, 7 September 1996 (B.A. Huber). San Miguel (near Celia), 1♂, July 1996 (R.L. Rodriguez). Tortuguero, at sea level, 4♂7♀, 23 September 1985 (R. Rojas & M. García) (UCR). Cerro Tortuguero, 3♂10♀, 8 August 1996 (B.A. Huber). Cocorí (30 km N Cariari), elev. 100 m, 3♂, January–March 1995 (E. Rojas)(INBIO). Cariari (17 km N Guapiles), 1♀, 3 March 1968 (C.E. Valerio) (UCR). *Prov. Heredia:* Finca La Selva (Biol. Station), elev. about 230 m, 17♂7♀, 10 January 1996 (B.A. Huber). Puerto Viejo, 1♂, 1–15 July 1965 (C.E. Valerio) (UCR). Estacion Barva, 1♂2♀, September 1996 (C. Viquez) (INBIO). *Prov. San José:* Quebrada González (35 km NNE San José), elev. about 500 m, 4♂1♀, 17 January 1996 (B.A. Huber). Zurquí (17 km NNE San José), elev. 1600 m, 14♂9♀, June–September 1995 (B.A. Huber & R.L. Rodriguez). Bajo la Hondura (15 km NE San José), elev. 1200–1500 m, 7♂3♀, 3 November 1995 (B.A. Huber), and 28 March 1981 (R. Briceño) (the latter in coll. UCR). *Prov. Alajuela:* Reserva Biologica San Ramón (25 km NW San Ramón), 8♂7♀, 18–19 March 1996 (B.A. Huber). San

Ramón de Alajuela, elev. 620 m, 1♂1♀, June-July 1994 (G. Hurtado) (INBIO). *Prov. Guanacaste:* Tilarán, 8♂9♀, 1 January 1969 (C.E. Valerio) (UCR). *Prov. Cartago:* El Cedral, Navarro, 1♀, 29 November 1979 (C.E. Valerio) (UCR). *Prov. Puntarenas:* Las Nubes de Sta Elena, Chirripó, elev. 1900 m, 1♂, 20 October 1995 (A. Pierdo) (INBIO). Uvita, Quebrada Colonia, about 3 km E Uvita village, elev. about 20–60 m, 3♂2♀, 14 February 1996 (B.A. Huber). Esquinas Rainforest, La Gamba, 8♂3♀, 2–3 July 1996 (B.A. Huber).

**Distribution.**—Known only from Costa Rica and Bocas del Toro Island, Panama.

Modisimus cahuita new species
(Figs. 24–35)

Type data.—Male holotype and female paratype from Cahuita, Prov. Limón, Costa Rica, 500 m S of village, at sea level, 13–15 June 1995 (B.A. Huber) (UCR).

Etymology.—Specific name from type locality.

Diagnosis.—Large dark species, distinguished from close relatives (*M. guatuso, M. tortuguero, M. sarapiqui, M. nicaraguensis*) by the paired protuberances on the epigynum (Figs. 34, 35), the two rows of spines on the male femora 1 and 2 (Fig. 32 - shared by *M. tortuguero*), and the few (0–4) modified hairs on each male chelicera (Fig. 25).

Description.—*Male:* Carapace grayish-ochre, slightly darker medially and on posterior part of eye turret. Clypeus without darker markings. Chelicerae and pedipalps brown. Sternum ochre-brown, lighter at lateral margins and medially. Legs brown, with slightly darker rings at femora (distally) and tibiae (proximally). Dark ring on femur followed by light ring. Tibiae distally yellowish. Opisthosoma dorsally grayish with black and white spots (Fig. 24) (white spots disappear in alcohol), ventrally with brown genital plate, long black stripe behind it, and another black spot before spinnerets. Six eyes on eye turret. Pedipalps as shown in Figs. 26–31, chelicerae with only 0–4 modified hairs on each side (Fig. 25). Femora 1 and 2 with two rows of spines ventrally (Fig. 32 - fem 1: about 30 spines in one row, about 6 in the other; fem 2: about 12 and 2 spines respectively). *Measurements of male holotype:* Total length: 3.2, prosoma length: 1.0, width: 1.2, opisthosoma length: 2.2; leg 1: fem: 9.7, pat: 0.6, tib: 9.3,
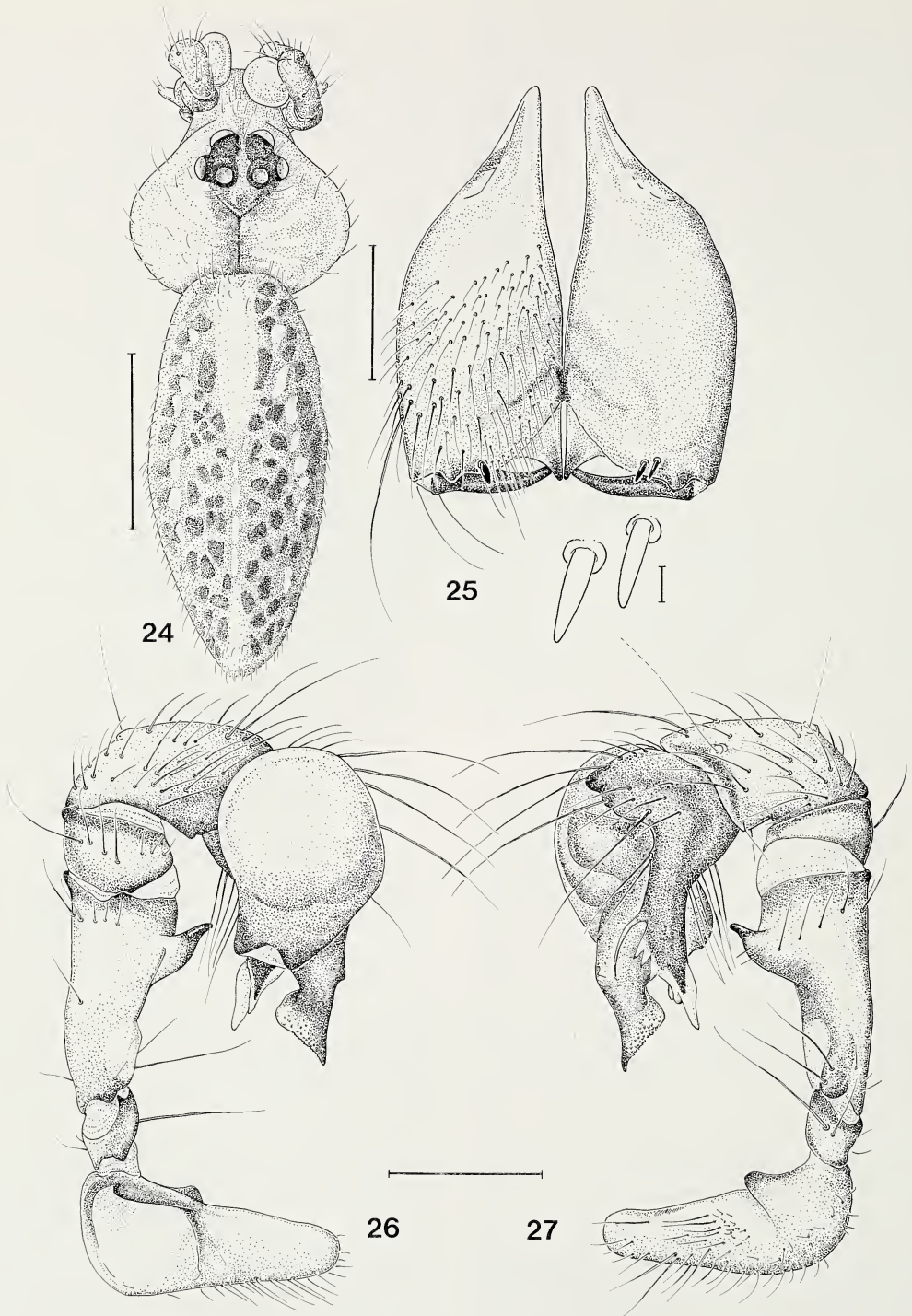
Figures 24–27.—*Modisimus cahuita* new species. 24, Male, dorsal view; 25, Male chelicerae, frontal view, with two modified hairs enlarged; 26, Left male pedipalp, slightly extended, prolateral view; 27, Left male pedipalp, slightly extended, retrolateral view. Scale bars = 1 mm (24); 0.2 mm (25); 0.01 mm (modified hairs); 0.3 mm (26, 27).
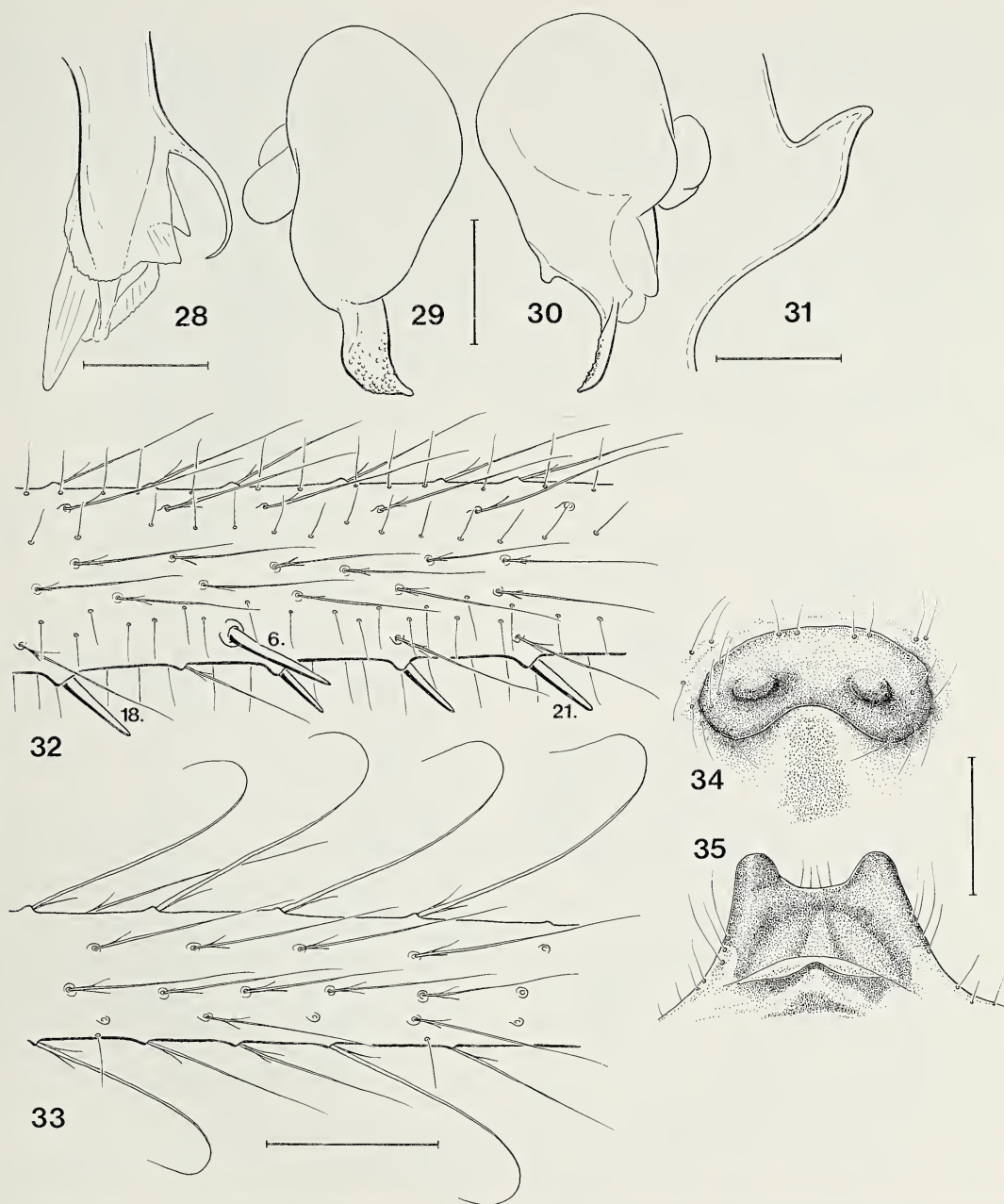
Figures 28–35.—*Modisimus cahuita* new species. 28, Left procursus, prolateral view; 29, Left bulb in ventral view; 30, Left bulb in prolateral view; 31, Palpal femur apophysis; 32, Male femur 1 in retrolateral view, showing spines 18–21 out of 30 from the prolateral row, and spine 6 out of 12 from the retrolateral row; 33, Male tibia 1 in retrolateral view; 34, Epigynum in ventral view; 35, Epigynum in posterior view. Scale bars = 0.1 mm (28, 31), 0.2 mm (29, 30, 32–35).

met: 17.1, tar: 2.8, total: 39.5, tibind: 65; leg 2: 25.8, leg 3: 19.7, leg 4: 22.4.

Female: Colors as in male, brown epigynum with two characteristic protuberances (Figs. 34, 35). Semithin serial sections of the epigynum revealed that these are not filled with glandular tissue but with a low epithelium and unspecific filling tissue. Legs lighter than in male. *Measurements of female paratype:* Total length: 3.4, prosoma length: 1.1,

width: 1.1, opisthosoma length: 2.3; leg 1: fem: 6.5, pat: 0.4, tib: 6.4, met: 11.7, tar: 2.0, total: 27.0, tibind: 67; leg 2: 16.8, leg 3: 12.7, leg 4: 14.8.

Tibia 1 in other material: Cahuita: 4♂: 8.4; 8.9; 9.2; 9.2. Hitoy Cerere: 3♂: 10.1; 10.1; 10.3; 3♀: 7.1; 7.2; 7.5.

Other material examined.—6♂2♀, and 1juv from type locality, same collection data as types. Hitoy Cerere Biological Reserve, at Rio Cerere, elev. about 150 m, Prov. Limón, Costa Rica, 3♂3♀, 8 September 1996 (B.A. Huber).

Distribution.—Known only from the two above mentioned localities in south-eastern Prov. Limón, Costa Rica.

Modisimus caldera new species
(Figs. 36–44)

Type data.—Male holotype and female paratype from the bank of Rio Caldera near Caldera, Prov. Chiriquí, Panama, elev. about 800 m, from small dome shaped webs under fallen leaves on the floor of open woodland near the river, 21 April 1995 (B.A. Huber) (UCR).

Etymology.—Specific name from type locality.

Diagnosis.—Small dark species, distinguished from close relatives (*M. coco*, *M. sanvito*) by the dark color, the form of the modified hairs on the male chelicerae (Fig. 43), and the pair of notches in the epigynum (Fig. 44 - the female of *M. coco* is not known).

Description.—*Male:* Carapace ochre with darker median stripe and eye turret. Clypeus brown, sternum ochre with a pair of longitudinal brown stripes. Legs ochre with brown rings on femora (distally), and tibiae (proximally and distally). Distal rings followed by light, almost white rings. Opisthosoma greenish-gray with black and small white spots (Fig. 36), ventrally bluish-gray, with brown genital plate and black spot behind it. Six eyes on eye turret, pedipalps as shown in Figs. 37–38, with distinctive procursi (Fig. 39), bulbs (Figs. 40, 41), and femur apophyses (Fig. 42). Chelicerae with one patch of characteristically formed hairs on each side (Fig. 43). Legs without spines. *Measurements of male holotype:* Total length: 2.2, prosoma length: 0.7, width: 0.8, opisthosoma length: 1.5; leg 1: fem: 4.6, pat: 0.3, tib: 4.5, met: 7.8, tar: 1.3, total: 18.5, tibind: 64; leg 2: 11.9, leg 3: 8.8, leg 4: 10.9.

Female: Colors as in male, epigynum brown, with distinctive notches posteriorly (Fig. 44). *Measurements of female paratype:* Prosoma length: 0.7, width: 0.8, (opisthosoma damaged); leg 1: fem: 3.7, pat: 0.3, tib: 3.7, met: 6.0, tar: 1.1, total: 14.8, tibind: 51; leg 2: 10.0, leg 3: 7.6, leg 4: 9.3.

Tibia 1 in the two other males: 4.8; 5.5.

Other material examined.—2♂ from type locality (same collection data as types).

Distribution.—Known only from type locality.

Modisimus coco new species
(Figs. 45–51)

Type data.—Male holotype from Bahia Wafer, Isla del Coco (Costa Rica), at sea level, May 1994 (Y. Camacho) (INBIO). Other material not known.

Etymology.—Species name from type locality.

Diagnosis.—Small light species, distinguished from light relatives (*M. bribri, M. sanvito*) by the stout and long dorsal spine on the procursus (Fig. 50 - *M. sanvito* has a very short dorsal spine: Fig. 122; *M. bribri* has a slender dorsal spine: Figs. 6–8).

Description.—*Male holotype:* Prosoma and opisthosoma pale ochre-yellow, only clypeus and palps slightly darker. Legs same color, without rings. Six eyes on low eye turret (Figs. 45, 46), pedipalps as in Figs. 47–48, procursus and femur apophysis as in Figs. 50–51, chelicerae as in Fig. 49, with short spines. *Measurements:* Total length: 2.0, prosoma length: 0.8, width: 0.9, opisthosoma length: 1.2; legs 1 and 2 missing, leg 3: 12.5, leg 4: 14.6.

Female: Female unknown.

Distribution.—Known only from type locality.

Modisimus dominical new species
(Figs. 52–60)

Type data.—Male holotype and female paratype from forest along creek, near the ground, about 1.5 km N Dominical, Prov. Puntarenas, Costa Rica, elev. about 10–100 m, 15 February 1996 (B.A. Huber, G. Huber, G. Roithinger) (UCR).

Etymology.—Species name from type locality.

**Diagnosis.**—Large dark species, easily dis-
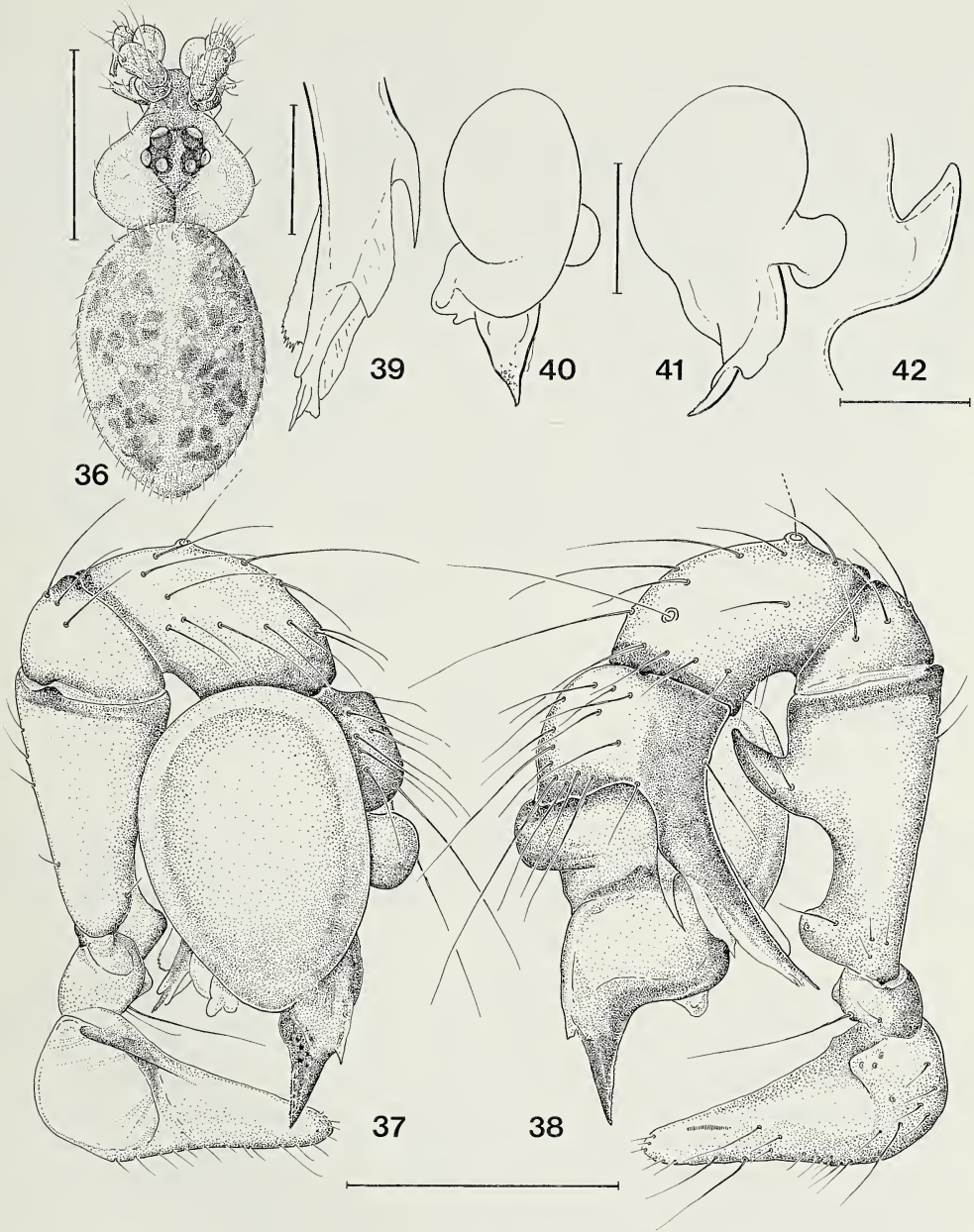
Figures 36–42.—***Modisimus caldera*** new species. 36, Male, dorsal view; 37, Left male pedipalp, slightly extended, and bulb rotated, prolateral view; 38, Left male pedipalp, slightly extended, and bulb rotated, retrolateral view; 39, Left procursus, prolateral view; 40, Left bulb in ventral view; 41, Left bulb in prolateral view; 42, Palpal femur apophysis. Scale bars = 1 mm (36); 0.3 mm (37, 38); 0.1 mm (39, 42); 0.2 mm (40, 41).

tinguished from congeners by the procursus that lacks a dorsal spine (Fig. 55), the form of the modified hairs on the male chelicerae (club-shaped - Fig. 59), and the wide epigynum with a pair of dark marks (Fig. 60). The Panamanian *M. pulchellus* is similar in several aspects, but the epigynum is rather triangular (Fig. 179), and the procursus does not end in two tips and has a small dorsal spine (Fig. 181).

Description.—*Male:* Carapace ochre, darker medially and on posterior side of eye
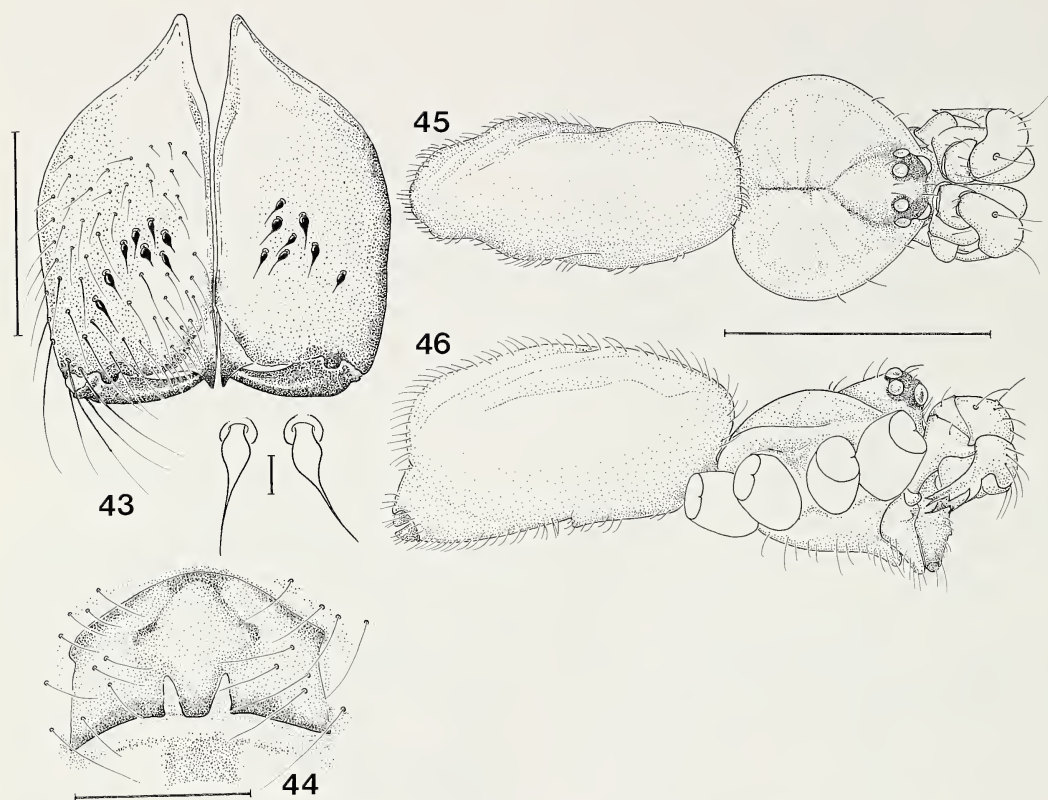
Figures 43–46.—New species of *Modisimus*. 43, 44. ***Modisimus caldera*** new species. 43, Male chelicerae, frontal view, with two modified hairs enlarged; 44, Epigynum, ventral view; 45, 46. ***Modisimus coco*** new species, male. 45, Dorsal view; 46, Lateral view. Scale bars = 0.2 mm (43, 44), 0.01 mm (modified hairs); 1 mm (45, 46).

turret, clypeus without markings, sternum brown with lighter ochre lateral margins and median stripe. Pedipalps and chelicerae ochre-brown. Legs ochre, with hardly visible darker rings on femora (distally) and tibiae (proximally and distally). Opisthosoma dorsally greenish-gray, with black and white spots (Fig. 52), ventrally with brown genital plate and black stripe behind it. Six eyes on eye turret, pedipalps as in Figs. 53–54, procursus, bulb and femur apophysis as in Figs. 55–58, chelicerae as in Fig. 59, with two patches of characteristic club-shaped hairs on each side, legs without spines. *Measurements of male holotype:* Total length: 3.1, prosoma length: 1.0, width: 1.3, opisthosoma length: 2.1; leg 1: fem: 10.4, pat: 0.6, tib: 10.1, met: 18.1, tar: 3.0, total: 42.2, tibind: 96; leg 2: 27.3, leg 3: 20.5, leg 4: 24.3.

Female: Colors mostly as in male, rings on legs more pronounced, with light rings follow-ing the distal dark rings. Opisthosoma ventrally with black stripe behind brown epigynum. Epigynum large, with a pair of dark marks anteriorly (Fig. 60). *Measurements of female paratype:* Total length: 3.5, prosoma length: 1.0, width: 1.1, opisthosoma length: 2.5; leg 1: fem: 6.5, pat: 0.4, tib: 6.7, met: 12.0, tar: 2.8, total: 28.4, tibind: 66; leg 2: 17.8, leg 3: 13.9, leg 4: 17.2.

Tibia 1 in other material: Dominical: 3♂: 8.7; 9.0; 9.4; 2♀: 6.8; 7.5. Uvita: 2♂: 9.3, 10.0, 4♀: 6.5, 6.7, 7,2, 7.4. Rincón de Osa: 2♀: 7.5, 7.8. Conte: 3♀: 6.4, 6.5, 6.8. Esquinas Rainforest: 7♂: 8.4–10.0 (x̄ = 9.2); 8♀: 6.6–7.5 (x̄ = 6.9). Wilson Gardens: 2♂: 8.6; 8.8; 5♀: 6.3–6.7 (x̄ = 6.5). San Vito: 1♀: 6.5.

Other material examined.—COSTA RICA. *Prov. Puntarenas:* 3♂2♀ from type locality, same collection data as types. Uvita, Quebrada Colonia, about 3 km E Uvita village, elev. about 20–60 m, 2♂5♀, 14 February 1996 (B.A. Huber). Esquinas
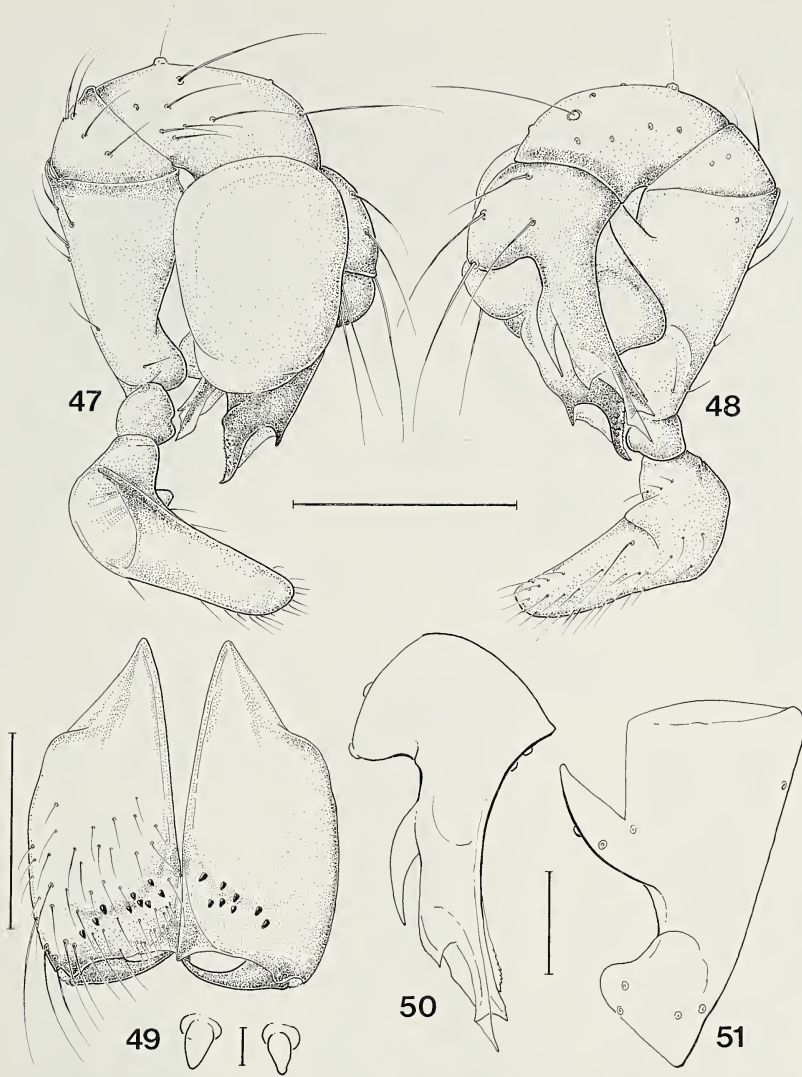
Figures 47–51.—*Modisimus coco* new species, male. 47, Left palp, prolateral view; 48, Left palp, retrolateral view; 49, Chelicerae, frontal view, with two modified hairs enlarged; 50, Left procursus, retrolateral view; 51, Left palpal femur, retrolateral view. Scale bars = 0.3 mm (47, 48), 0.2 mm (49–51), 0.01 mm (modified hairs).

Rainforest, La Gamba, 7♂8♀, 2–3 July 1996 (B.A. Huber), and 2♀ from same locality, 10 August 1995 (R.L. Rodriguez). Wilson Botanical Gardens, 4 km S San Vito de Coto Brus, 4♂5♀, 5 July 1996 (B.A. Huber). San Vito de Coto Brus, 1♀, 1 juv, 4 July 1996 (B.A. Huber). Rincón de Osa, 2♀, 1 juv, 19 February–13 March 1967 (C.E. Valerio) (UCR). Conte, Punta Burica, 1♂3♀, 12–13 July 1984 (C.E. Valerio & R. Solís) (UCR).

Distribution.—Known only from the mentioned localities in southern Prov. Puntarenas, Costa Rica.

Modisimus guatuso new species
(Figs. 61–94)

Type data.—Male holotype and female paratype from forest near Bajo La Hondura (15 km NE San José) Prov. San José, Costa Rica, elev. about 1200–1500 m, near the ground in humid, shaded declivities, April–November 1995 (B.A. Huber & R.L. Rodriguez) (UCR).

**Etymology.**—Named for the Guatuso, an indigenous Costa Rican people.
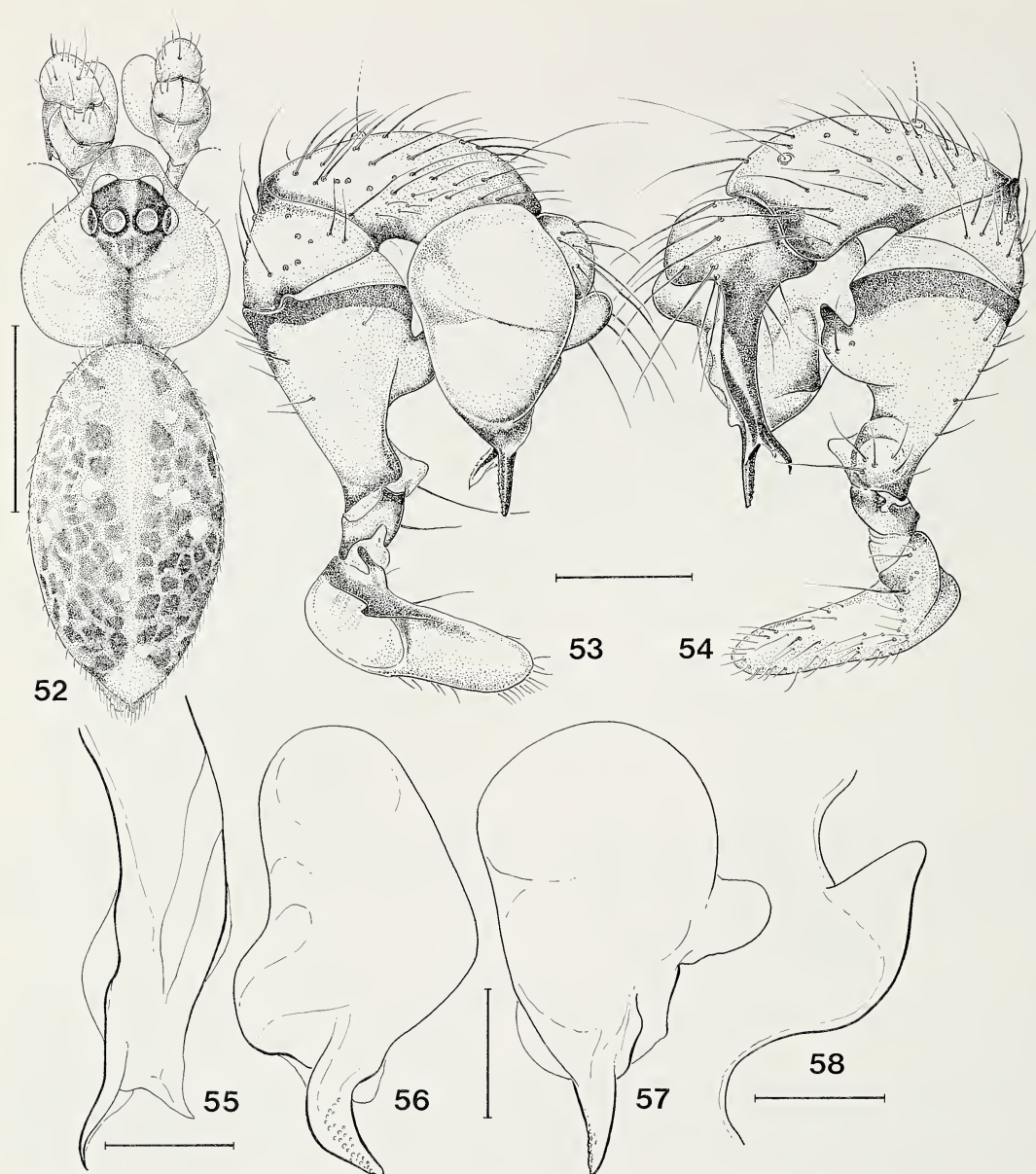
Figures 52–58.—*Modisimus dominical* new species. 52, Male, dorsal view; 53, Left male pedipalp, slightly extended, prolateral view; 54, Left male pedipalp, slightly extended, retrolateral view; 55, Left procursus, prolateral view; 56, Left bulb, ventral view; 57, Left bulb, prolateral view; 58, Palpal femur apophysis. Scale bars = 1 mm (52); 0.3 mm (53, 54); 0.1 mm (55, 58), 0.2 mm (56, 57).

Diagnosis.—Dark species, variable in size and morphology. Morphologically similar to the light *M. bribri*. Distinguished from other close relatives by the simple flat epigynum (Figs. 89–94 - *M. cahuita* and *M. sarapiqui* have projections on the epigynum: Figs. 34, 35, 133, 134; *M. nicaraguensis* has a deep in-

dentation posteriorly: Fig. 109), and the spines on the male femur 1 (missing or up to about 15 in one row; *M. tortuguero* has two rows with a total of about 40 spines).

Description.—*Male holotype:* Carapace ochre-brown, darker medially and on posterior side of eye turret, clypeus as carapace, pedi-
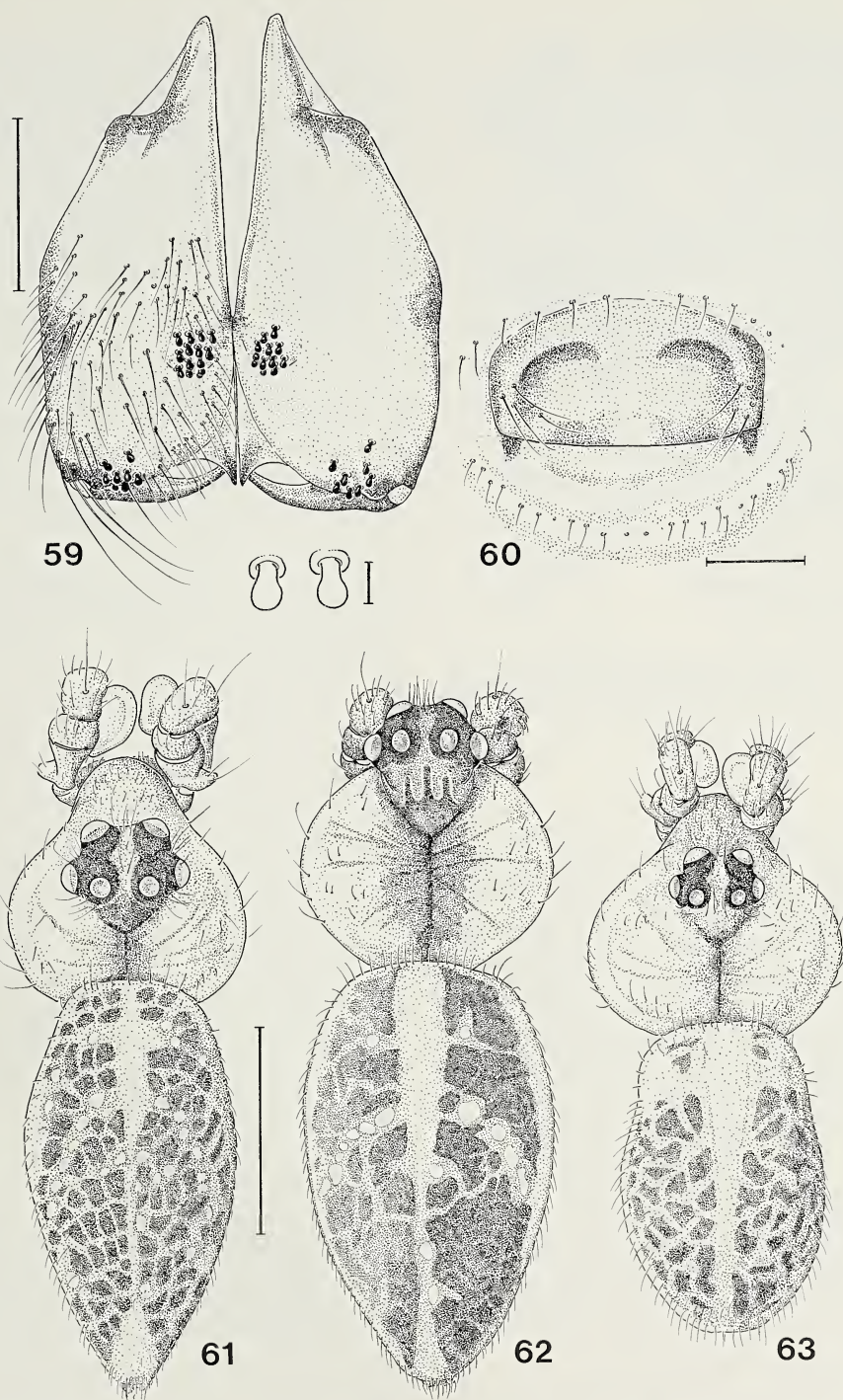
Figures 59–63.—New species of *Modisimus*. 59, **Modisimus dominical** new species, male chelicerae, frontal view, with two modified hairs enlarged; 60, **M. dominical** new species, epigynum, ventral view; 61–63. **Modisimus guatuso** new species, males in dorsal view (note the differences in shape of the prosoma, due largely to differences in the angle of view). 61, Bajo La Hondura (type locality); 62, Lagito (Arenal); 63, Alto Jaramillo. Scale bars = 0.2 mm (59, 60), 0.01 mm (modified hairs); 1 mm (61–63).
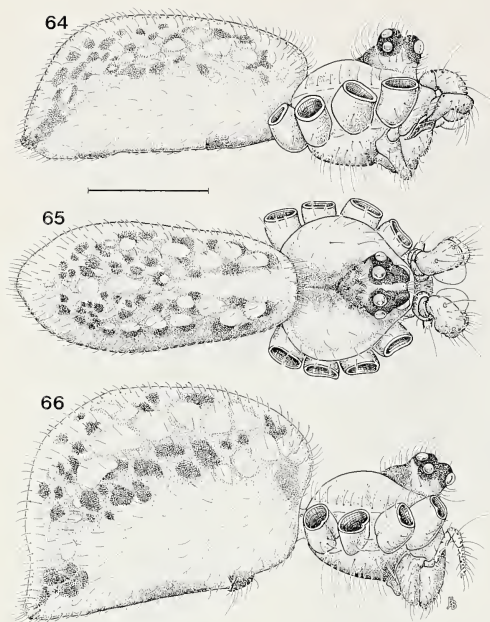
Figures 64–66.—*Modisimus guatuso* new species, specimens from Reserva Biol. Leonel Oviedo. 64, Male, lateral view; 65, Male, dorsal view; 66, Female, lateral view. Scale bar = 1 mm.

palps and chelicerae brown, sternum brown with lighter ochre lateral margins and median stripe. Legs ochre-brown, with dark rings on femora (distally) and tibiae (proximally and distally). Opisthosoma dorsally greenish-gray with large black and smaller white spots in characteristic pattern (Fig. 61), ventrally with brown genital plate, black stripe behind it and another dark spot before spinnerets. Six eyes on eye turret, pedipalps as shown in Figs. 67–68, procursus, bulb and femur apophysis as in Figs. 69, 75–76, 81. Chelicerae with two patches of modified hairs on each side (Fig. 86). Femora 1 and 2 with a row of a spines ventrally. *Measurements:* Total length: 3.1, prosoma length: 1.1, width: 1.2, opisthosoma length: 2.0; leg 1: fem: 7.2, pat: 0.4, tib: 7.2, met: 12.9, tar: 2.3, total: 30.0, tibind: 65; leg 2: 19.2, leg 3: 15.0, leg 4: 17.2.

Female paratype: Colors as in male, but opisthosoma ventrally only with black stripe behind brown epigynum (Fig. 89). Legs without spines. *Measurements:* Total length: 3.1, prosoma length: 1.0, width: 1.1, opisthosoma length: 2.1; leg 1: fem: 5.9, pat: 0.4, tib: 5.9, met: 10.0, tar: 2.4, total: 24.6, tibind: 49; leg 2: 16.2, leg 3: 12.6, leg 4: 14.9.

Variation.—Variation within populations is usually small and does not pose taxonomic problems, whereas inter-population variation is significant to a degree that originally I ascribed species status to several of the populations now included in this species. The reason to lump them was that the characters showed no correlated variation and several intermediate forms were found by more intense collecting. Still, some populations are included with hesitation (e.g., some Costa Rican Central Valley populations, or that from Alto Jaramillo, Panama), and may well turn out to be reproductively isolated from each other and from the population at the type locality. Only statistical analyses on larger samples and/or biological experiments may eventually justify or reject the present limitation.

Usually the spiders and their webs were found near the ground in humid, shaded habitats between buttresses or other objects. More rarely, the spiders lived in small webs under fallen leaves (Alto Jaramillo), or between twigs in shrubs and small trees about 20–50 cm above the ground (Reserva Biol. Leonel Oviedo). In Turrialba, I found them under corrugated sheet iron, in the grass layer.

Individuals in some populations are among the largest *Modisimus* (e.g., Arenal area, see below), while others are relatively small (e.g., Alto Jaramillo, see below). It must be noted, however, that even within one area, size can vary significantly between collection dates (e.g., Bajo La Hondura, see below), or within a sample from one day (e.g., Cahuita, see below). The most common pattern on the opisthosoma is that shown in Figs. 61–62. Different patterns occur in the Alto Jaramillo (Panama) population (Fig. 63 - it is not clear whether the lack of white spots is an artifact, caused by ethanol), and in some Central Valley (Costa Rica) populations (Fig. 65). Generally, this character is difficult to assess because white spots tend to disappear in ethanol. The male femur 1 is often set with a row of spines, up to about 15, very rarely with two rows, but then with only a few spines in the retrolateral row; in several populations (e.g., Quebrada González, Reserva Biol. Leonel Oviedo), males have no spines on their femora, and in a few (e.g., Bajo la Hondura, Arenal area) there are males with and without spines. The male chelicerae are provided with either one or two patches of spines on each
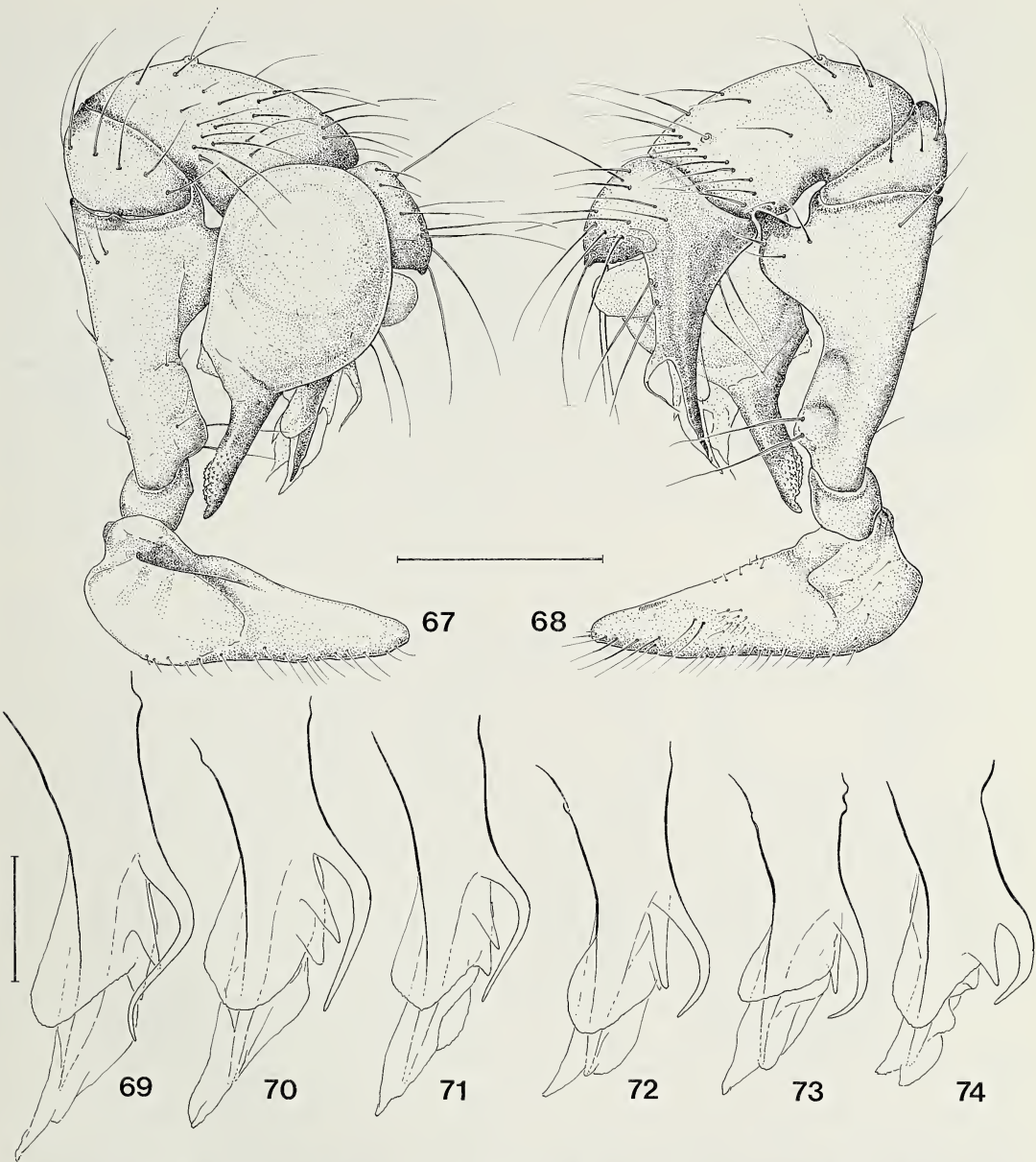
Figures 67–74.—***Modisimus guatuso*** new species. Left pedipalp, slightly extended, and bulb rotated. 67, Prolateral view; 68, Retrolateral view; 69–74. Left procursus, prolateral view. 69, Bajo La Hondura (type locality); 70, Tortuguero; 71, Uvita; 72, Reserva Biol. Leonel Oviedo; 73, Cahuita; 74, Alto Jaramillo. Scale bars = 0.3 mm (67, 68); 0.1 mm (69–74).

side (Figs. 86, 87), or with an intermediate pattern (e.g., Fig. 88). The spines are never characteristically formed (as in some other species, Figs. 43, 59, 117).

The procursus varies both in size and shape (Figs. 69–74). It must be noted, however, that some of the variation shown may be artificial, as most of the distal structures on the procur-sus are membranous. Apart from variation in size, the bulb shows little variation (Figs. 75–80). However, the bulb of several other species is very similar (Figs. 9–12, 144–145), which renders the bulb of little diagnostic value. The pedipalpal femur apophysis varies as shown in Figs. 81–85. The epigynum never shows any protrusions, but is a simple, though
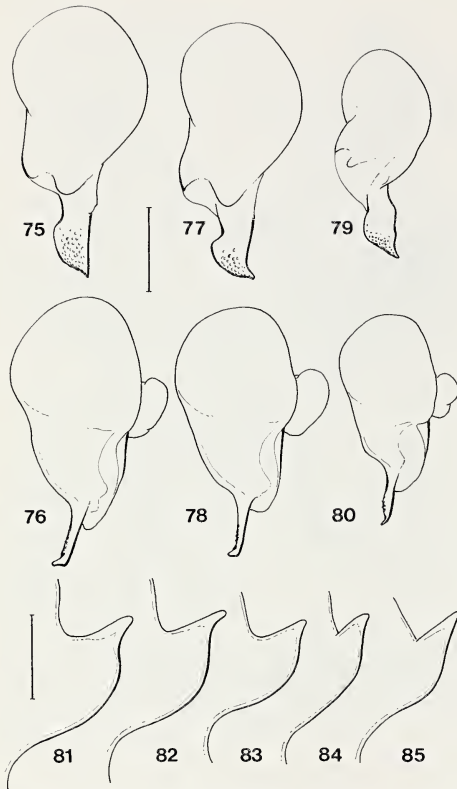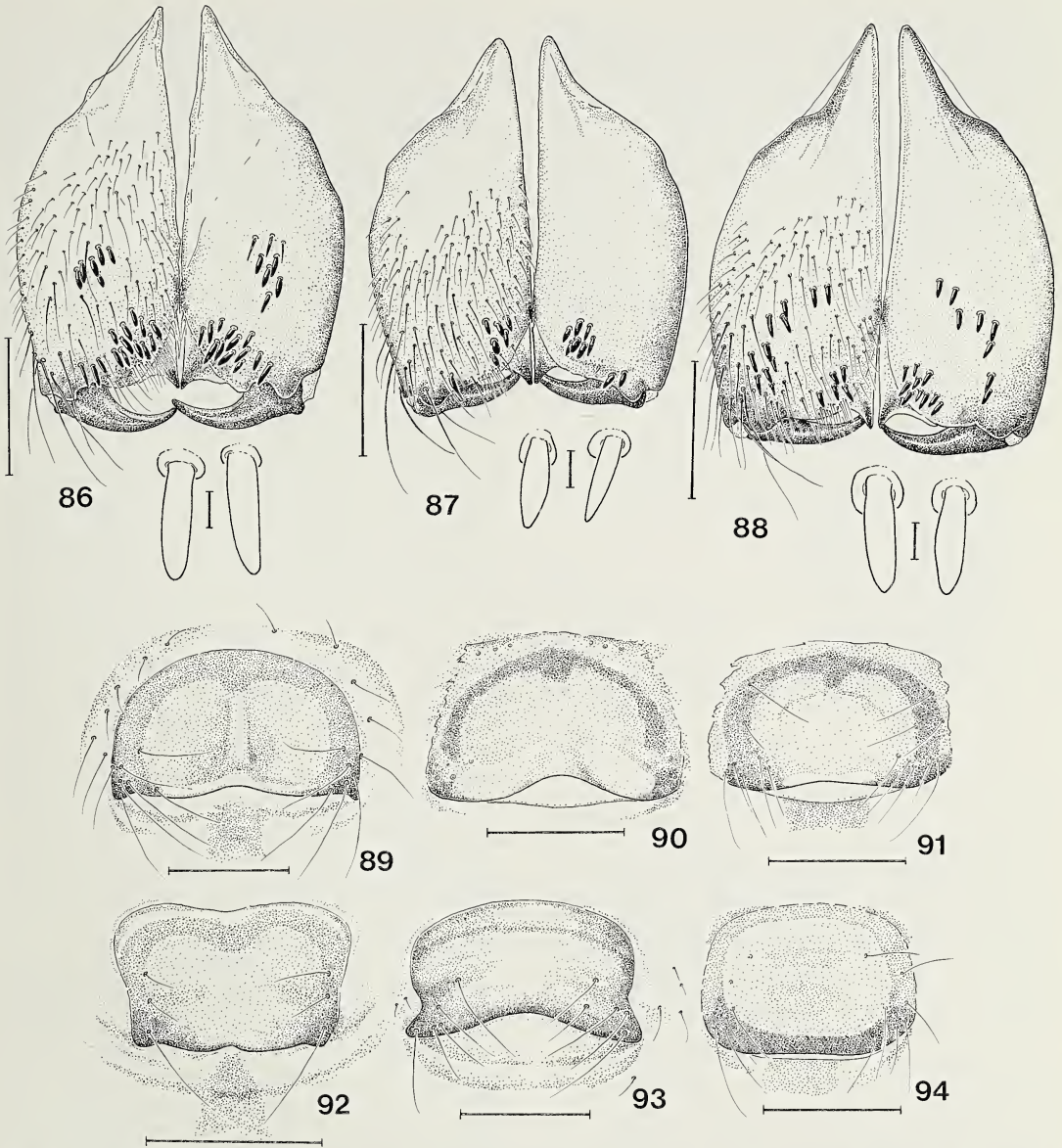
Figures 75–85.—*Modisimus guatuso* new species. 75–80. Left genital bulb in ventral view (above) and retrolateral view (below). 75, 76, Bajo La Hondura (type locality); 77, 78, Volcan Cacao; 79, 80, Turrialba. 81–85. Palpal femur apophysis. 81, Bajo La Hondura (type locality); 82, Tortuguero; 83, Alto Jaramillo; 84, Cahuita; 85, Turrialba. Scale bars = 0.2 mm (75–80); 0.1 mm (81–85).

highly variable, sclerotized plate (Figs. 89–94).

Tibia 1 in other material: Bajo La Hondura (April–November 1995): 8♂: 6.9–7.9 ($\bar{x}$ = 7.3), 7♀: 4.0–5.7 ($\bar{x}$ = 5.2). Bajo La Hondura (28 March 1981): 9♂: 4.6–5.9 ($\bar{x}$ = 5.3), 16 females: 3.2–4.1 ($\bar{x}$ = 3.7). Reserva Biol. Leonel Oviedo: 12♂: 5.3–7.1 ($\bar{x}$ = 6.5), 13♀: 4.1–5.7 ($\bar{x}$ = 4.8). San Antonio de Escazú: 7♂: 6.4–7.8 ($\bar{x}$ = 7.3), 6♀: 4.5-5.6 ($\bar{x}$ = 4.9). Monterrey: 1♀: 4.3. Zurquí: 2♂: 6.5; 7.9, 1♀: 5.3. Quebrada González: 1♂: 7.5; 1♀: 5.2. San Francisco de Dos Rios: 1♂: 5.1. Rio Paraca: 1♀: 5.7. San Ramón: 6♂: 8.0–9.2 ($\bar{x}$ = 8.4), 8♀: 5.4–6.5 ($\bar{x}$ = 5.9). Arenal area (Lagito, Cascada, Tabacon): 13♂: 7.7–9.5 ($\bar{x}$ = 8.7), 5♀: 5.0–6.5 ($\bar{x}$ = 6.0). El Venado: 3♂: 6.8, 7.2, 7.7, 3♀: all 4.8. Bosque Rio La Hoga: 2♀: 4.8, 4.9. Finca La Selva: 6♂: 6.5–8.8 ($\bar{x}$ = 7.5); 4♀: 5.1; 5.4; 5.4; 5.8. Guayabo and Alto de Varas: 5♂: 6.5–9.1 ($\bar{x}$ = 7.6). Tapantí: 1♂: 6.5; 1♀: 5.2. Turrialba: 1♂: 5.9, 8♀: 3.8–4.2 ($\bar{x}$ = 4.0). Tortuguero: 1♂: 8.0, 2♀: 5.7, 6.4. Siquirres: 1♂: 9.1; 2♀: 6.1, 6.5. Cahuita: 3♂: 9.9; 6.8; 4.3; 2♀: 5.0; 3.6. Puerto Vargas: 1♀: 5.2. Hitoy Cerere: 2♂: 7.9, 10.6; 4♀: 5.1, 5.4, 6.7, 7.0. Carara: 1♂: 7.7, 1♀: 5.4. Uvita: 5♂: 6.7–7.8 ($\bar{x}$ = 7.4); 1♀: 5.4. Manuel Antonio: 10♂: 6.1–7.5 ($\bar{x}$ = 6.9); 7♀: 4.5–5.5 ($\bar{x}$ = 4.9). La Gamba: 4♀: 4.5, 4.8, 4.8, 4.9. Wilson Gardens: 2♂: 7.2, 7.7; 1♀: 5.1. Conte: 1♂: 6.9, 1♀: 4.4. Hacienda La Josefina: 3♀: 4.9, 5.0, 5.4. Volcán Cacao: 3♂: 7.4, 7.8, 8.0; 4♀: 5.0, 5.1, 5.2, 5.7. Bocas del Toro: 5♂: 7.1–9.3 ($\bar{x}$ = 8.2); 6♀: 4.4–5.7 ($\bar{x}$ = 5.1). Alto Jaramillo: 17♂: 4.2–5.3 ($\bar{x}$ = 4.7); 5♀: 3.0–3.6 ($\bar{x}$ = 3.3). Bluefields: 4♂: 6.1, 6.6, 7.0, 7.4; 4♀: 3.8, 4.5, 4.6, 4.6.

Other material examined.—COSTA RICA: *Prov. San José:* Numerous ♂ & ♀ from type locality, same collection data as types; and 9♂19♀ from type locality, 28 March 1981 (G. Umaña, M. Santana, V. Zelendon, E. Alvarado, M.M. González) (UCR). Reserva Biol. Leonel Oviedo ("bosquecito") in the Universidad de Costa Rica, elev. about 1150 m, numerous males and females, February–September 1995 (B.A. Huber). San Antonio de Escazú (about 8 km WSW San José), elev. about 1300–1400 m, 9♂6♀, 30 May 1995 (B.A. Huber). Monterrey, 1♀, 21 April 1967 (C.E. Valerio) (UCR). Zurquí, (17 km NNE San José), elev. 1600 m, 2♂1♀, 14 September 1995 (B.A. Huber). Quebrada González (35 km NNE San José), elev. about 500 m, 1♂1♀, 17 January 1996 (B.A. Huber). Rio Paraca, Villa Colon, 1♀, 2 November 1968 (C.E. Valerio) (UCR). La Colina, San Francisco de Dos Rios, 1♂, May 1981 (C.Gómez) (UCR). *Prov. Alajuela:* Reserva Biol. San Ramón, (25 km NW San Ramón), 7♂8♀, 18–19 March 1996 (B.A. Huber). San Ramón de Dos Rios, 1.5 km N Finca Nueva Zelandia, elev. 620 m, 2♂9♀, February–July 1995 (F.A. Quesada & A. Picado) (INBIO). Around Lagito, a small lake at the northern slope of Volcán Arenal, elev. about 620 m, 4♂4♀, 5 October 1995 (B.A. Huber). La Cascada, 6 km SW Fortuna, elev. about 520 m, 8♂1♀, 4 October 1995 (B.A. Huber). Tabacon, about 6 km WNW Fortuna, elev. about 480 m, 1♀, 3 October 1995 (B.A. Huber). El Venado, San Carlos, 3♂3♀, January 1980 (C.E. Valerio) (UCR). San Ramón de Alajuela, elev. 620–1100 m, 3♂1♀, June 1994–February 1995 (G. Hurtado & G. Carballo) (INBIO). *Prov. Heredia:* Finca La Selva (Biol. Station), elev. about 230 m, 4♂4♀, 10 January 1996 (B.A. Huber). Bosque Rio La Hoga, San Rafael, 3♀, no date (UCR). San Joaquín,

Figures 86–94.—*Modisimus guatuso* new species. 86–88. Male chelicerae, frontal view, with two modified hairs enlarged. 86, Bajo La Hondura (type locality); 87, Alto Jaramillo; 88, Lagito (Arenal). 89–94. Epigyna, ventral view. 89, Bajo La Hondura (type locality); 90, Bocas del Toro; 91, Manuel Antonio; 92, Alto Jaramillo; 93, Reserva Biol. Leonel Oviedo; 94, Tortuguero. Scale bars = 0.2 mm (modified hairs: 0.01 mm).

1♂1♀, 10 July 1995 (C. Viquez) (INBIO). *Prov. Cartago:* Turrialba, elev. about 600 m, about 1 km E of town, along the old railway, 1♂8♀, 15 March 1996 (B.A. Huber). Tapantí, about 3 km S Tapantí village, near the Rio Orosi, elev. about 1400 m, 1♂1♀, 8 January 1996 (B.A. Huber). Tapantí, elev. 1150 m, 1♀, November 1994 (G. Mora) (INBIO). Guayabo and Alto de Varas, 5♂, 18 April and 9 May 1981 (M.M. González and UCR spider course)

(UCR). Grano de Oro, Chirripó, elev. 1120 m, 1♂, September 1993 (P. Campos) (INBIO). Madreselva, Finca Los Lagos, elev. 2000–2600 m, 1♂4♀, September-October 1995 (M.M. Chavarría) (INBIO). *Prov. Limón:* Fila Carbon, about 2 km SW Cahuita, elev. about 10–50 m, 3♂2♀, 15 June 1995 (B.A. Huber). Puerto Vargas, Cahuita, 1♀, 8–14 March 1966 (C.E. Valerio) (UCR). Tortuguero, at sea level, 1♂2♀, 25 November 1985 (R. Rojas) and 4–5 Feb-

ruary 1982 (C.E. Valerio) (UCR). Cerro Tortuguero, at sea level, 1♂6♀, 8 August 1996 (B.A. Huber). Cerro Cocori (30 km N Cariari), elev. 100 m, 1♀, November-December 1994 (E. Rojas) (INBIO). Siquirres, at Rio Pacuare, 1♂2♀, 9 September 1996 (B.A. Huber). Hitoy Cerere Biol. Reserve, elev. 150–200 m, 3♂4♀, 7–8 September 1996 (B.A. Huber), and 1♂ from same locality, January-March 1994 (G. Carballo) (INBIO). Rara Avis, elev. 540–700 m, 1♀, July 1996 (R.L. Rodriguez). *Prov. Puntarenas:* San Luis, Monteverde, elev. 1000–1350 m, 11♂7♀, January 1993–April 1995 (Z. Fuentes) (INBIO). Estacion La Casona, Monteverde, elev. 1520 m, 3♂, July-September 1995 (K. Martinez) (INBIO). Reserva Biologica Carara, elev. about 50 m, 1♂1♀, 12 January 1996 (B.A. Huber), and 30 November–3 December 1982 (A.C. Gómez) (UCR). Altamira, Sendero Educativo, elev. 1150–1400 m, 3♂, November 1994 (R. Delgado & M. Segura) (INBIO). Wilson Botanical Gardens, 4 km S San Vito de Coto Brus, 2♂3♀, 5 July 1996 (B.A. Huber). Cerro Pittier, elev. 1750 m, 6♂6♀, 8 June 1995 (parataxonomist's course) (INBIO). Uvita, Quebrada Colonia, about 3 km E Uvita village, elev. about 20–60 m, 5♂2♀, 14 February 1996 (B.A. Huber). Manuel Antonio, elev. about 20–60 m, 12♂8♀, 13–14 January 1996 and 7 December 1996 (B.A. Huber), and 3♂6♀ from same locality, elev. 10–20 m, December 1990-July 1991 (G. Varela & R. Zuñiga) (INBIO). Esquinas Rainforest, La Gamba, 4♀, 2–3 July 1996 (B.A. Huber). Conte, Punta Burica, 1♂4♀, 12–13 July 1984 (C.E. Valerio & R. Solís) (UCR). Rancho Quemado, Peninsula de Osa, elev. 200 m, 12♂14♀, October 1993–March 1994 (A.L. Marín & A.H. Gutierrez) (INBIO). Estacion Sirena, Sendero Espaveles, elev. 0–10 m, 1♂, April 1995 (B. Gamboa & A. Picado) (INBIO). *Prov. Guanacaste:* Hacienda La Josefina, 6 km SWS Cerro Cacao, elev. about 560 m, 3♀, 19 December 1973 (W. Sibaja, L. Hilje, C.E. Valerio) (UCR). Volcán Cacao, 3♂6♀, July 1996 (R.L. Rodriguez). Pitilla Biol. Station (9 km S Sta. Cecilia), 4♂7♀, May 1994–April 1995 (P. Rios) (INBIO). **PANAMA.** *Prov. Bocas del Toro:* Bocas del Toro Island, in the forest at sea level, 7♂7♀, 23 April 1995 (B.A. Huber). *Prov. Chiriquí:* Alto Jaramillo (near Boquete, 40 km N David), 20♂9♀, 21 April 1995 (B.A. Huber). **NICARAGUA.** *Dept. Zelaya Sur:* Pancasan near Bluefields, 4♂4♀, 6 October 1996 (B.A. Huber).

Distribution.—Known from Nicaragua, Costa Rica, and Panama.

Remark.—The natural history of this species has been studied previously by Briceño (1985), Eberhard & Briceño (1983, 1985 sub "*M.* sp. C") (population at the Reserva Biol. Leonel Oviedo), and Eberhard (1992) (population at La Selva).

Modisimus madreselva new species
(Figs. 95–100)

Type data.—Male holotype from Madreselva, Finca Los Lagos, Prov. Cartago, Costa Rica, elev. 2000–2600 m, 28 June–10 July 1993 (M.M. Chavarría) (INBIO 2416).

Etymology.—Specific name from type locality.

Diagnosis.—Small light species, distinguished from close relatives by the short dorsal spine and its position on the procursus (Fig. 95 - *M. bribri* has a long, slender spine: Figs. 6–8; in *M. sanvito* the dorsal spine is situated much more proximally: Fig. 122).

Description.—*Male:* Entire body very light, prosoma and legs ochre-yellow, opisthosoma rather grayish. Legs with darker rings on femora (distally), and tibiae (proximally and distally). Habitus like in *M. sanvito* new species (Fig. 119), with six eyes on eye turret in much the same configuration. Procursus with distinctive dorsal spine (arrow in Fig. 95), palpal femur apophysis as in Fig. 96, bulb as in Figs. 97–98, chelicerae with two sets of modified hairs on each side (Fig. 99). Legs without spines. *Measurements of male holotype:* Total length: 2.4, prosoma length: 0.9, width: 1.0, opisthosoma length: 1.5; leg 1: fem: 6.8, pat: 0.3, tib: 7.0, met: 11.8, tar: 2.0, total: 27.9, tibind: 74; leg 2: 18.6, leg 3: 13.2, leg 4 missing.

Female: Colors as in male, opisthosoma with brown eggs shining laterally through cuticle, epigynum with arch (Fig. 100) that is often greenish. Two of the females have a rather dark opisthosoma, one of these has large white spots dorsally on the opisthosoma. *Measurements of a female* (type locality; INBIO 2894): Total length: 2.0, prosoma length: 0.7, width: 0.8, opisthosoma length: 1.3; leg 1: fem: 4.1, pat: 0.3, tib: 4.1, met: 6.7, tar: 1.6, total: 16.8, tibind: 59; leg 2: 11.5, leg 3: 8.9, leg 4: 10.6.

Tibia 1 in other material: Madreselva: 1♂: 6.7; 1♀: 4.6. Cuerici: 2♂: 6.2, 7.2; 5♀: 4.8–5.2 (x̄ = 5.0).

Other material examined.—2♂4♀ from type locality, July 1993–October 1995, other collection data as in types (INBIO). Cuerici, Prov. Cartago, Costa Rica, elev. 2600 m, 2♂6♀, September 1995–June 1996 (A. Picado) (INBIO).

Distribution.—Known only from the two
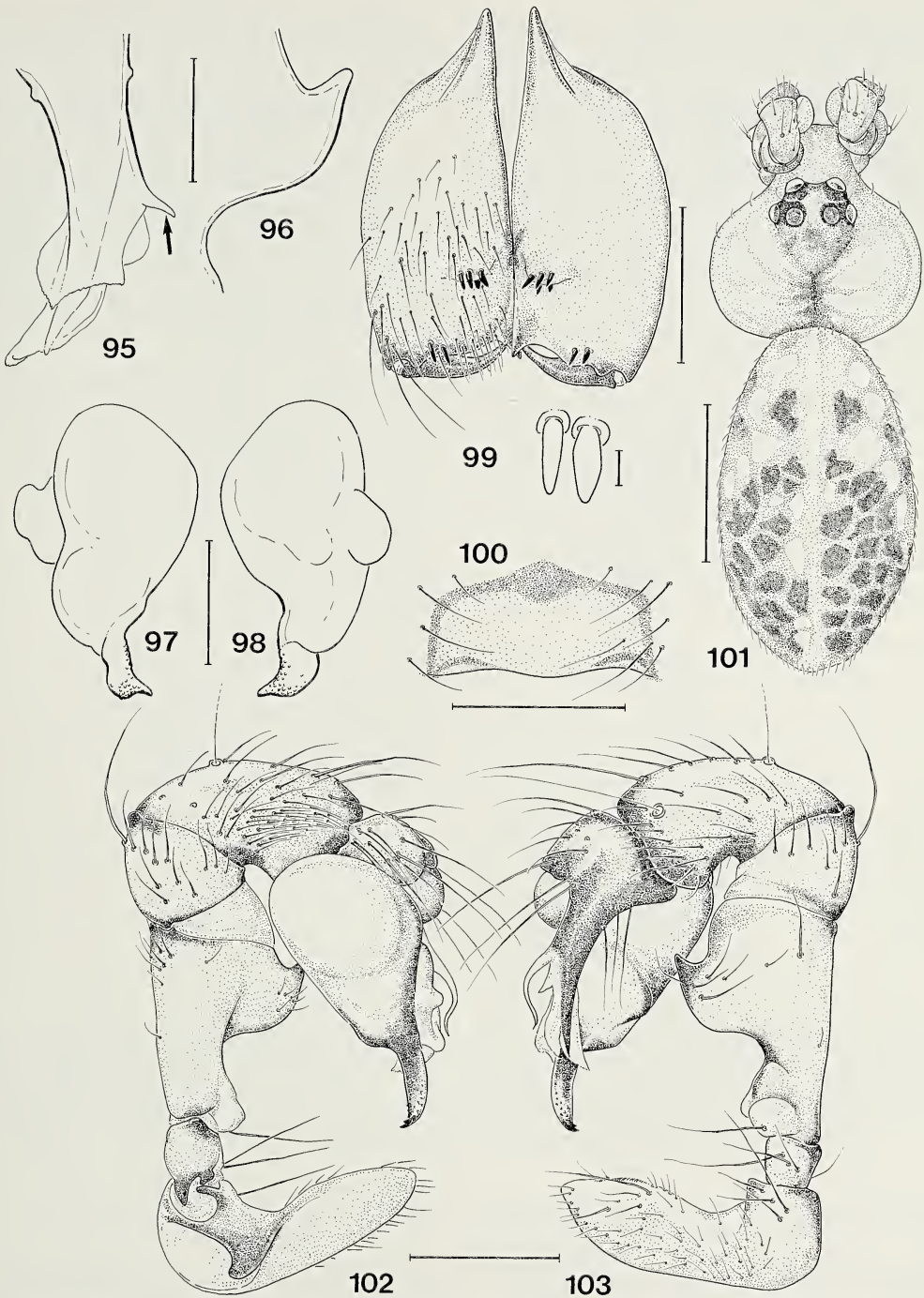
Figures 95–103.—New species of *Modisimus*. 95–100. **Modisimus madreselva** new species. 95, Left procursus, prolateral view (arrow: dorsal spine); 96, Palpal femur apophysis; 97, Left bulb in ventral view; 98, Left bulb in dorsal view; 99, Male chelicerae, frontal view, with two modified hairs enlarged; 100, Epigynum, ventral view. 101–103. **Modisimus nicaraguensis** new species. 101, Male, dorsal view; 102, Left pedipalp, slightly extended, prolateral view; 103, Left pedipalp, slightly extended, retrolateral view. Scale bars = 0.1 mm (95, 96); 0.2 mm (97–100); 0.01 mm (modified hairs); 1 mm (101); 0.3 mm (102, 103).

mentioned localities in the Sierra de Talamanca, Costa Rica.

Modisimus nicaraguensis new species
(Figs. 101–109)

Type data.—Male holotype and female paratype from La Selva Negra, a forest about 12 km N Matagalpa, Dept. Matagalpa, Nicaragua, elev. about 1300 m, in twigs of small undergrowth, about 0.5 m above the ground, 24 July 1995 (B.A. Huber) (UCR).

Etymology.—Named for the Republic of Nicaragua.

Diagnosis.—Large dark species, distinguished from close relatives by the flat epigynum with posterior indentation (Fig. 109 - *M. guatuso* lacks the indentation: Figs. 89–94; *M. cahuita* and *M. sarapiqui* have protrusions on the epigynum: Figs. 34, 35, 133, 134), and by the lack of spines on the male femur 1 (*M. tortuguero* has about 40 spines on each femur 1).

Description.—*Male:* Carapace ochre, darker medially and on posterior side of eye turret, clypeus without markings, sternum unicolored ochre-yellow, pedipalps and chelicerae brown. Legs ochre-brown, with darker rings on femora (distally) and tibiae (proximally and distally). Opisthosoma dorsally very dark, with black and white spots (Fig. 101), ventrally with brown genital plate, black stripe behind it and smaller brown spot before spinnerets. Six eyes on eye turret, pedipalps as in Figs. 102, 103, procursus, bulb and femur apophysis as in Figs. 104–107. Chelicerae as in Fig. 108, legs without spines. *Measurements of male holotype:* Total length: 3.7, prosoma length: 1.3, width: 1.4, opisthosoma length: 2.4; leg 1: fem: 7.9, pat: 0.6, tib: 7.7, met: 13.6, tar: 2.5, total: 32.3, tibind: 56; leg 2: 22.2, leg 3: 16.4, leg 4: 19.6. *Tibia 1 in two other males:* 7.5; 7.9.

Female: Colors mostly as in male, opisthosoma ventrally only with black stripe behind brown epigynum which has a characteristic posterior indentation (Fig. 109). *Measurements of female paratype:* Total length: 3.5, prosoma length: 1.0, width: 1.1, opisthosoma length: 2.5; leg 1: fem: 5.4, pat: 0.4, tib: 5.4, met: 9.1, tar: 2.2, total: 22.5, tibind: 46; leg 2: 15.1, leg 3: 11.7, leg 4: 14.1.

Other material examined.—Two males from type locality, same collection data as types.

Distribution.—Known only from type locality.

Modisimus pittier new species
(Figs. 110–118)

Type data.—Male holotype and female paratype from Cerro Pittier (about 30 km N San Vito de Coto Brus), Prov. Puntarenas, Costa Rica, elev. 1750 m, 8 June 1995 (collected by a parataxonomist's course) (INBIO).

Etymology.—Specific name from type locality.

Diagnosis.—Large dark species, easily distinguished from congeners by the two dorsal spines on the procursus (Figs. 113, 114), the spiral apophysis on the bulb (Figs. 111, 112, 115), and the large epigynum (Fig. 118 - resembling only that of *M. dominical*: Fig. 60).

Description.—*Male:* Carapace grayish-ochre, darker at median line and eye turret. Clypeus with dark stripe (Fig. 110). Chelicerae and pedipalps brown. Sternum ochre-brown, lighter at lateral margins and medially. Legs brown, with slightly darker rings on femora (distally) and tibiae (proximally and distally). Opisthosoma dorsally dark greenish-gray, with light pattern that may originally have been set with white spots (Fig. 110), ventrally with prominent brown genital plate, short black stripe behind it, without black spot before spinnerets. Six eyes on eye turret. Pedipalps as shown in Figs. 111–112, procursus of distinctive shape (Figs. 113, 114), bulb with bulbal apophysis and another, spirally wound apophysis (Figs. 111, 112, 115), chelicerae with characteristically formed modified hairs (Fig. 117). Legs without spines. *Measurements of male holotype:* Total length: 3.4, prosoma length: 1.1, width: 1.5, opisthosoma length: 2.4; leg 1: fem: 10.0, pat: 0.6, tib: 10.0, met: 17.2, tar: 2.9, total: 40.7, tibind: 79; leg 2: 27.2, leg 3: 21.8, leg 4: 26.1.

Female: Colors as in male, with large brown epigynum (Fig. 118). *Measurements of female paratype:* Total length: 3.3, prosoma length: 1.1, width: 1.2, opisthosoma length: 2.2; leg 1: fem: 7.2, pat: 0.5, tib: 7.3, met: 12.2, tar: 2.5, total: 29.7, tibind: 66; leg 2: 20.2, leg 3: 15.9, leg 4: 19.3. *Tibia 1 in female from Alto Jaramillo:* 5.4.

Other material examined.—Alto Jaramillo (near Boquete, 40 km N David, Prov. Chiriquí, Pan-
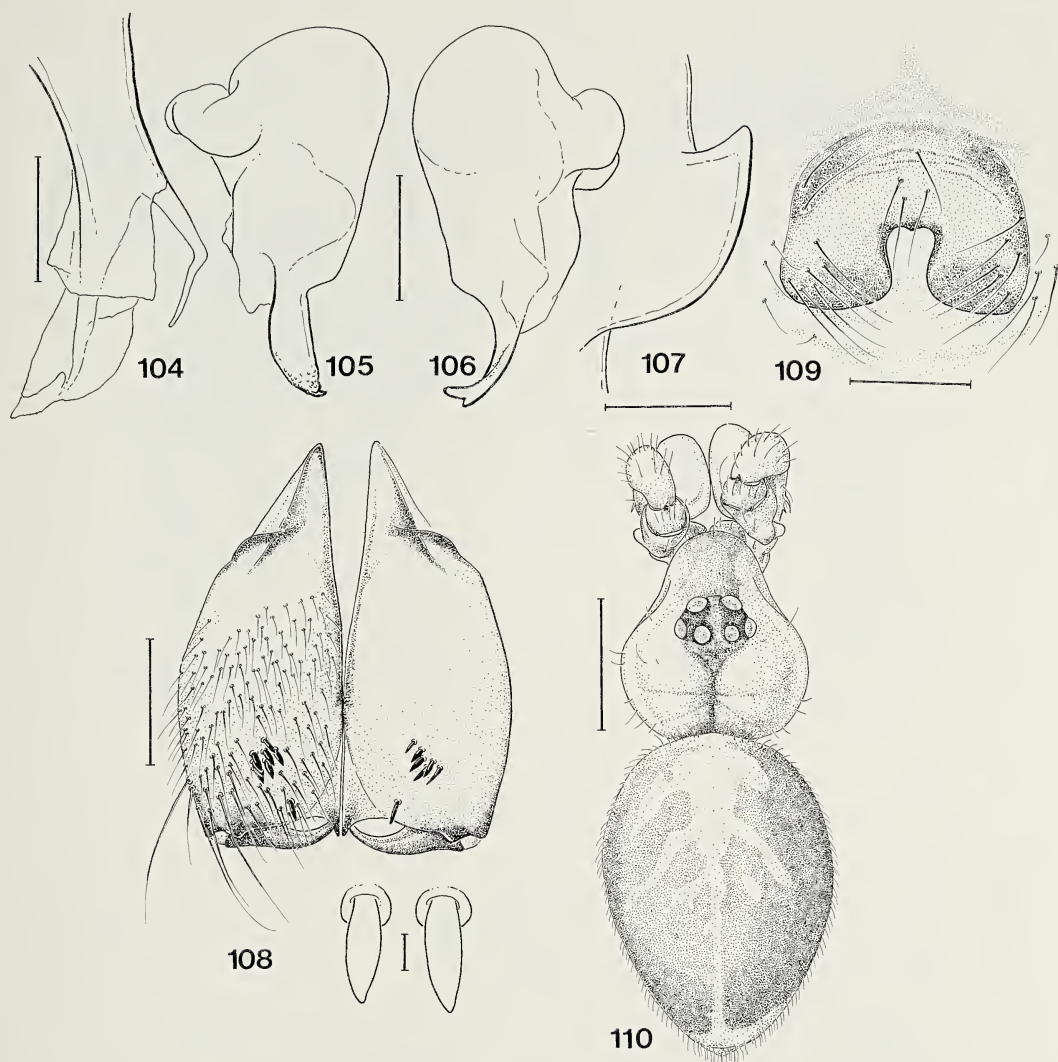
Figures 104–110.—New species of *Modisimus*. 104–109. **Modisimus nicaraguensis** new species. 104, Left procursus, prolateral view (dorsal spine artificially bent); 105, Left bulb, ventral view; 106, Left bulb, prolateral view; 107, Palpal femur apophysis; 108, Male chelicerae, frontal view, with two modified hairs enlarged; 109, Epigynum, ventral view; 110, **Modisimus pittier** new species, male, dorsal view. Scale bars = 0.1 mm (104, 107), 0.2 mm (105, 106, 108, 109); 0.01 mm (modified hairs); 1 mm (110).

ama), elev. about 1100 m, 1♀, 21 April 1995 (B.A. Huber).

Distribution.—Known only from the two above mentioned localities in the Costa Rican and Panamanian Cordillera de Talamanca.

Modisimus sanvito new species
(Figs. 119–127)

Type data.—Male holotype and two female paratypes from San Vito de Coto Brus, Prov. Puntarenas, Costa Rica, 14–20 March 1967 (C.E. Valerio) (UCR). Other material not known.

Etymology.—Species name from type locality.

Diagnosis.—Small light species, distinguished from close relatives by separated black rings of eyes (Fig. 119), and the short dorsal spine on the procursus and its position (Fig. 122 - *M. coco* has a long dorsal spine: Fig. 50; *M. madreselva* has the spine more distally: Fig. 95).
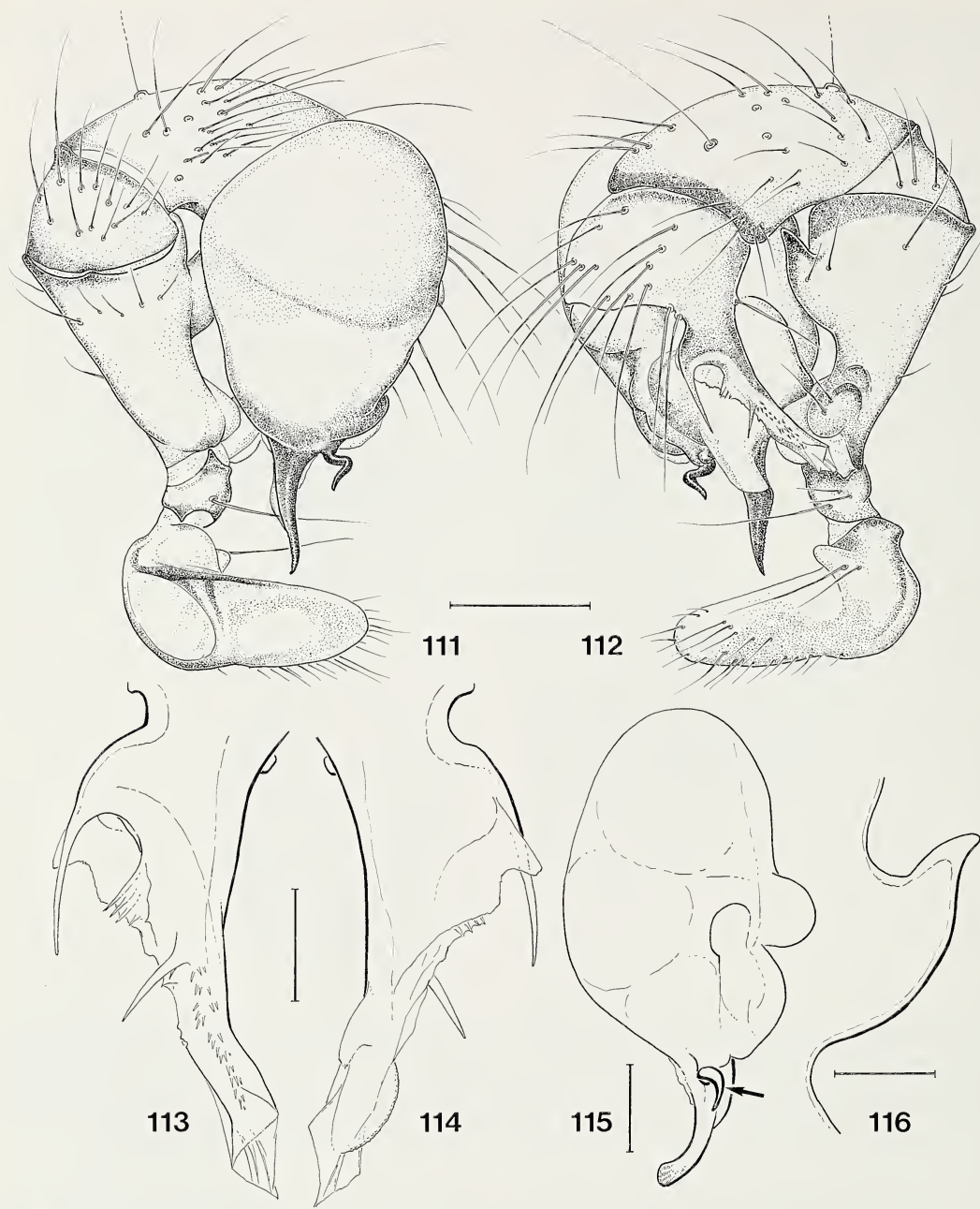
Figures 111–116.—*Modisimus pittier* new species. 111, Left pedipalp in prolateral view; 112, Left pedipalp in retrolateral view; 113, Left procursus, retrolateral view; 114, Left procursus, prolateral view; 115, Bulb, dorsal view (arrow: spiral apophysis); 116, Palpal femur apophysis. Scale bars = 0.3 mm (111, 112); 0.1 mm (113, 116); 0.2 mm (114, 115).

Description.—*Male:* Prosoma ochre-yellow, only rings around eyes black. Legs ochre-yellow with hardly visible darker rings on femora (distally) and tibiae (proximally and distally). Opisthosoma pale ochre. Six eyes on eye turret. Pedipalps as shown in Figs. 120–121, procursus, bulb and femur apophysis as in Figs. 122–125, chelicerae with 8 small modified hairs of each side, some of which are situated on a sclerotized ridge (Fig.
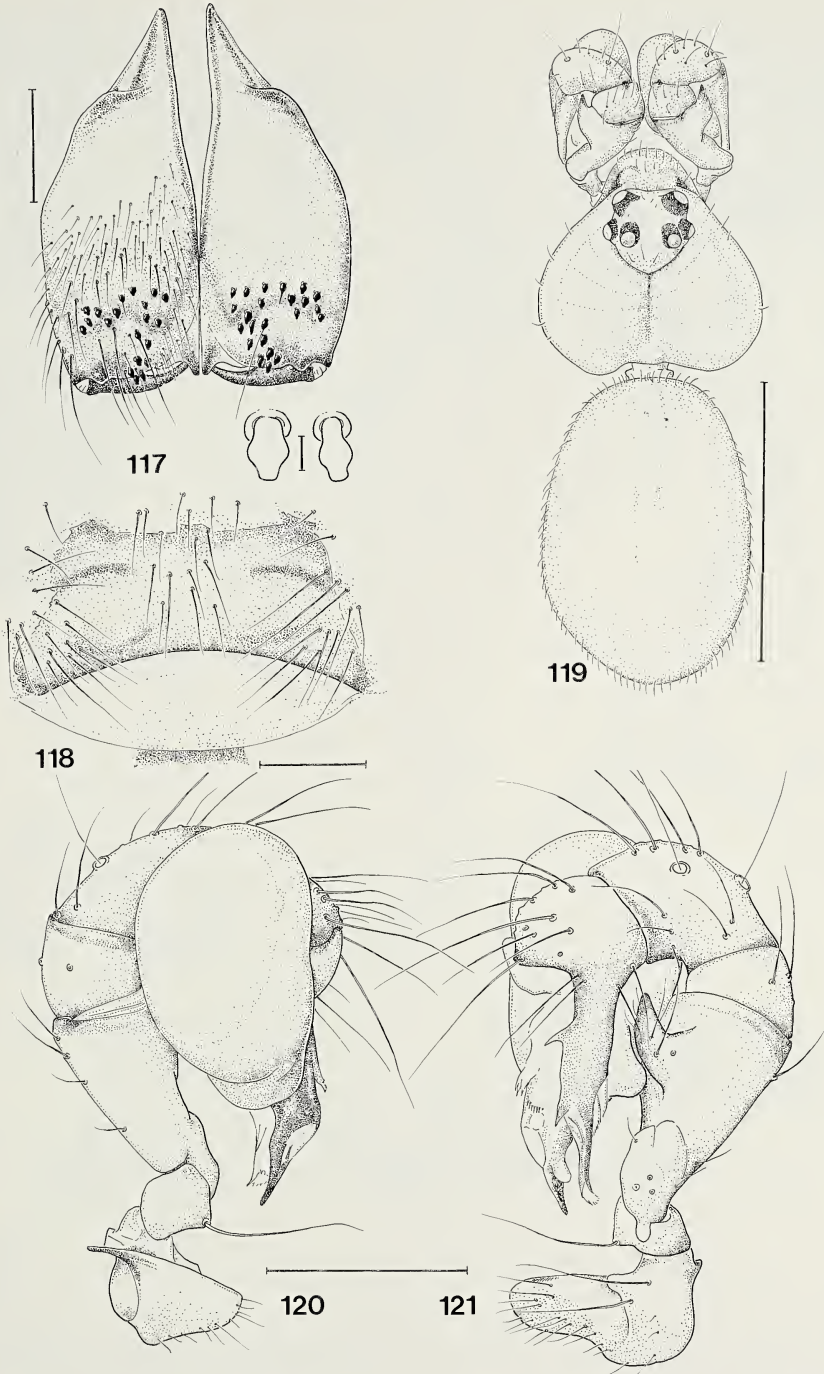
Figures 117--121.—New species of *Modisimus*. 117, 118. **Modisimus pittier** new species. 117, Male chelicerae, frontal view, with two modified hairs enlarged; 118, Epigynum, ventral view; 119–121. **Modisimus sanvito** new species. 119, Male, dorsal view; 120, Left pedipalp, prolateral view; 121, Left pedipalp, retrolateral view. Scale bars = 0.2 mm (117, 118); 0.01 mm (modified hairs); 1 mm (119); 0.3 mm (120, 121).
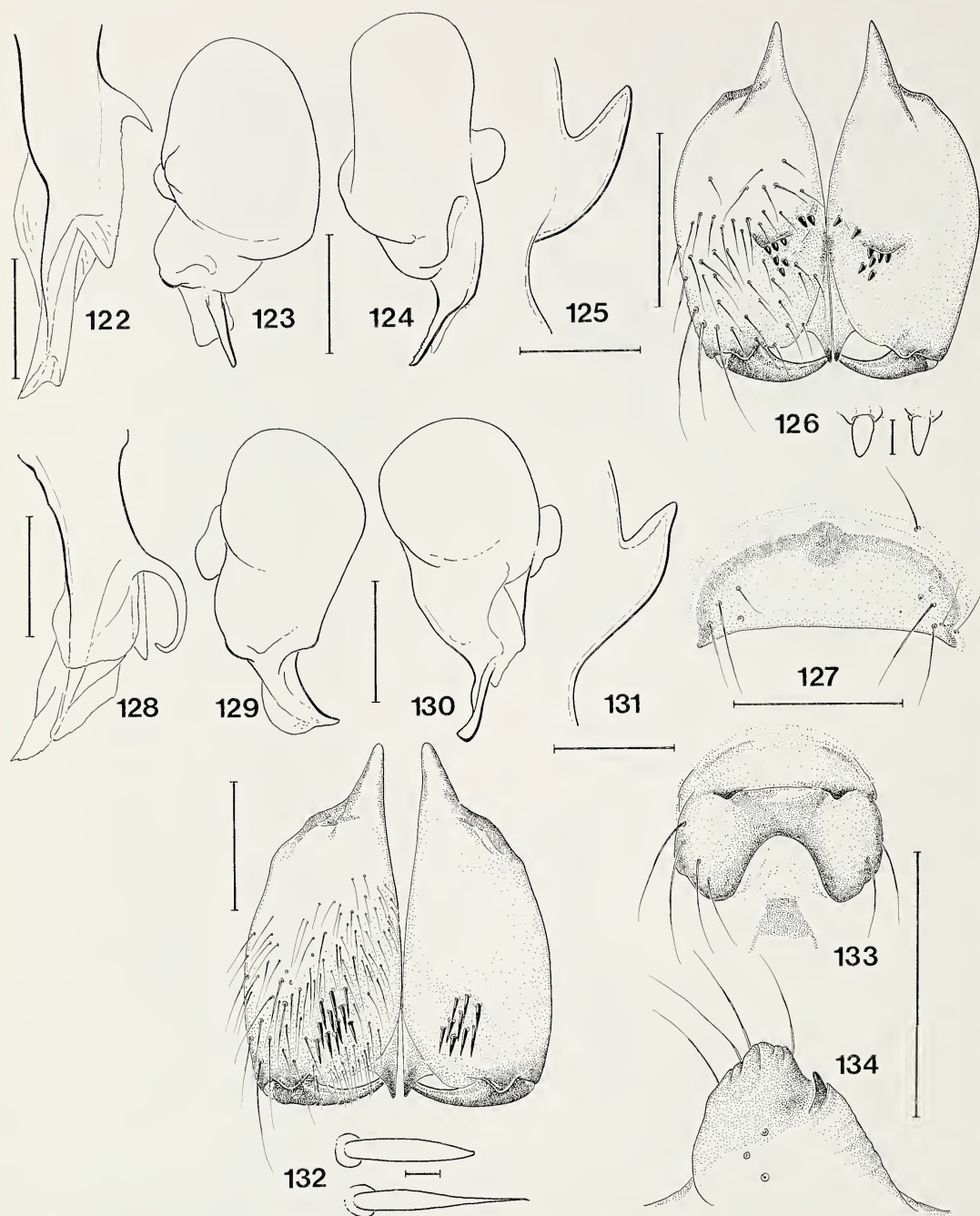
Figures 122–134.—New species of *Modisimus*. 122–127. **Modisimus sanvito** new species. 122, Left procursus, prolateral view; 123, Left bulb in ventral view; 124, Left bulb in prolateral view; 125, Palpal femur apophysis; 126, Male chelicerae, frontal view, with two modified hairs enlarged; 127, Epigynum, ventral view. 128–134. **Modisimus sarapiqui** new species. 128, Left procursus, prolateral view; 129, Left bulb, ventral view; 130, Left bulb, prolateral view; 131, Palpal femur apophysis; 132, Male chelicerae, frontal view, with two modified hairs enlarged; 133, Epigynum, ventral view; 134, Epigynum, lateral view. Scale bars = 0.1 mm (122, 125, 128, 131); 0.2 mm (123, 124, 126, 127, 129, 130, 132–134); 0.01 mm (modified hairs).
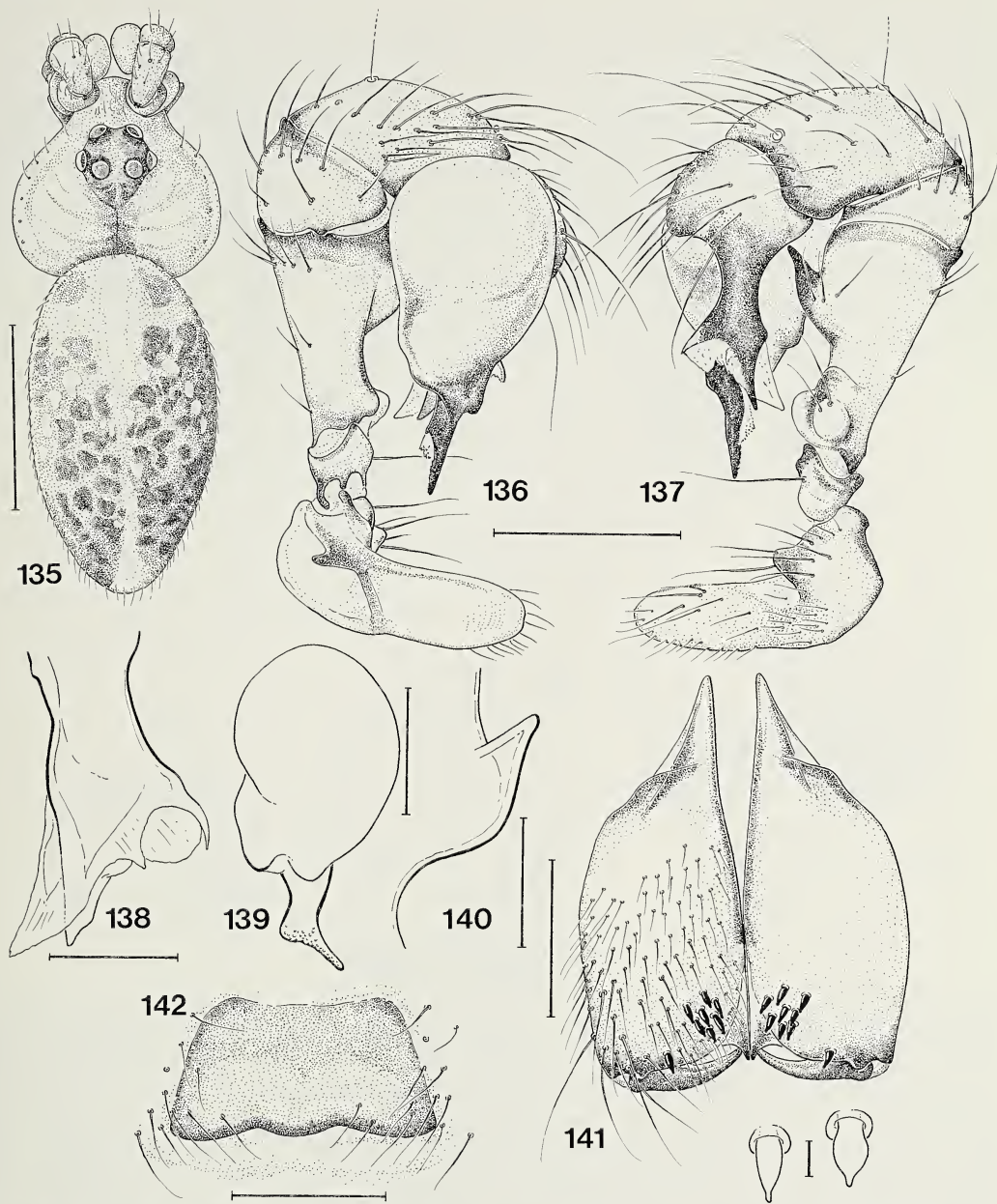
Figures 135–142.—***Modisimus selvanegra*** new species. 135, Male, dorsal view; 136, Left pedipalp, slightly extended, prolateral view; 137, Left pedipalp, slightly extended, retrolateral view; 138, Left procursus, prolateral view; 139, Left bulb, ventral view; 140, Palpal femur apophysis; 141, Male chelicerae, frontal view, with two modified hairs enlarged; 142, Epigynum, ventral view. Scale bars = 1 mm (135); 0.3 mm (136, 137); 0.1 mm (138, 140); 0.2 mm (139, 141, 142); 0.01 mm (modified hairs).

126). Legs without spines. *Measurements of male holotype:* Total length: 1.8, prosoma length: 0.7, width: 0.8, opisthosoma length: 1.1; leg 1: fem: 6.4, pat: 0.3, tib: 6.4, met: 12.0, tar: 1.7, total: 26.8, tibind: 81; leg 2: 17.6, leg 3: 11.2, leg 4: 14.3.

Female: Colors as in male. Epigynum (Fig. 127) slightly darker. *Measurements of a female paratype:* Total length: 2.2, prosoma length: 0.7, width: 0.8, opisthosoma length: 1.5; leg 1: fem: 4.8, pat: 0.3, tib: 4.6, met: 7.7, tar: 1.7, total: 19.1, tibind: 66; leg 2: 12.0, leg
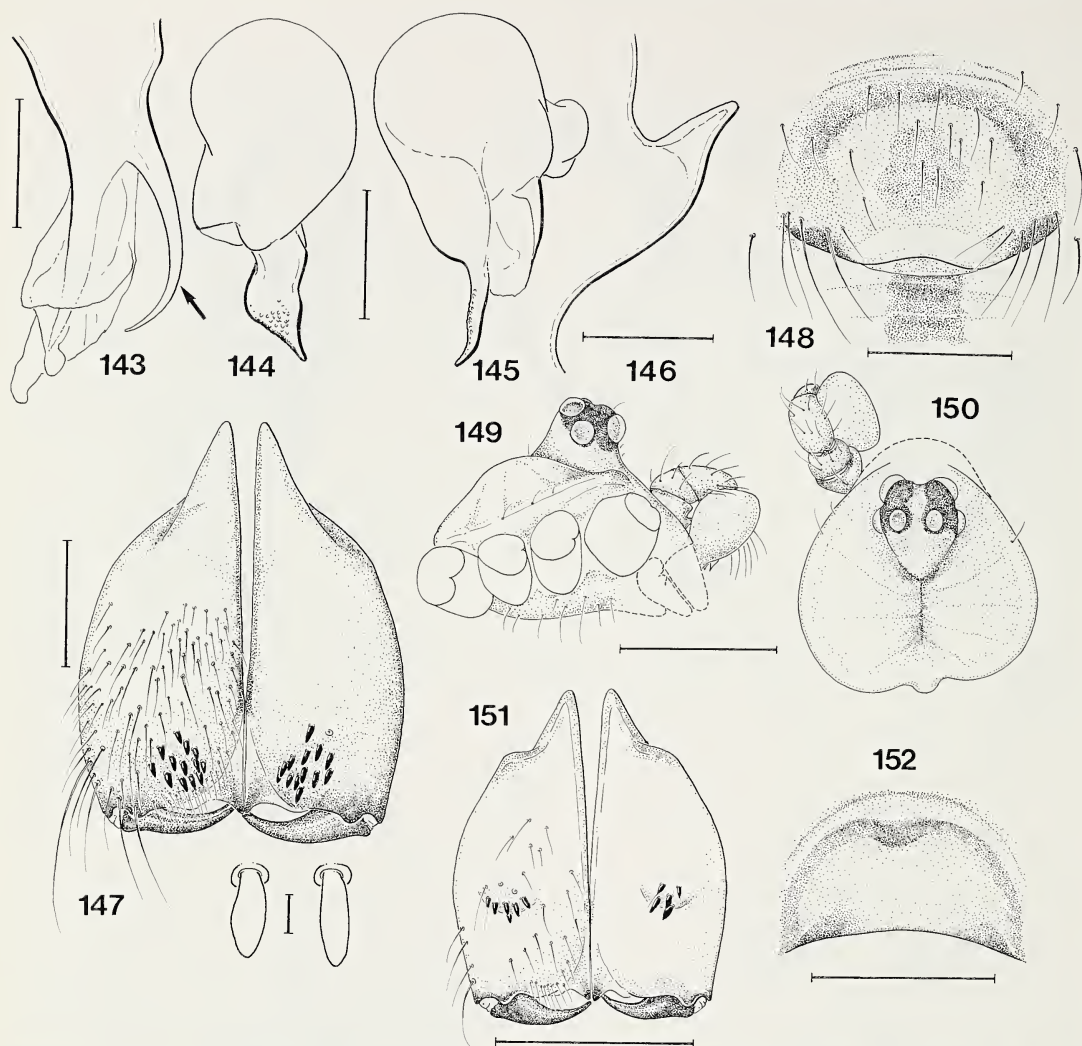
Figures 143–152.—Species of *Modisimus*. 143–148. **Modisimus tortuguero** new species. 143, Left procursus, prolateral view (arrow: dorsal spine); 144, Left bulb in ventral view; 145, Left bulb in prolateral view; 146, Palpal femur apophysis; 147, Male chelicerae, frontal view, with two modified hairs enlarged; 148, Epigynum, ventral view. 149–152. *Modisimus dilutus* Gertsch. 149, Male prosoma, lateral view (dashed line: type damaged); 150, Male prosoma, dorsal view (dashed line: type damaged); 151, Male chelicerae, frontal view; 152, Epigynum, ventral view. Scale bars = 0.1 mm (143, 146); 0.2 mm (144, 145, 147, 148, 151, 152); 0.5 mm (149, 150); 0.01 mm (modified hairs).

3: 8.5, leg 4: 10.9. *Tibia 1 in other female:* 4.3.

Distribution.—Known only from type locality.

Modisimus sarapiqui new species
(Figs. 128–134)

Type data.—Female (!) holotype, male and (damaged) female paratypes from Puerto Viejo de Sarapiqui, Prov. Heredia, Costa Rica,

elev. about 40 m, 1–5 July 1965 (C.E. Valerio) (UCR).

Etymology.—Species name from type locality.

Diagnosis.—Large dark species with characteristic protruding epigynum (Figs. 133, 134). Otherwise similar to *M. guatuso*, *M. tortuguero* and *M. cahuita*.

Description.—*Male paratype:* Carapace ochre-brown, darker medially and on pos-
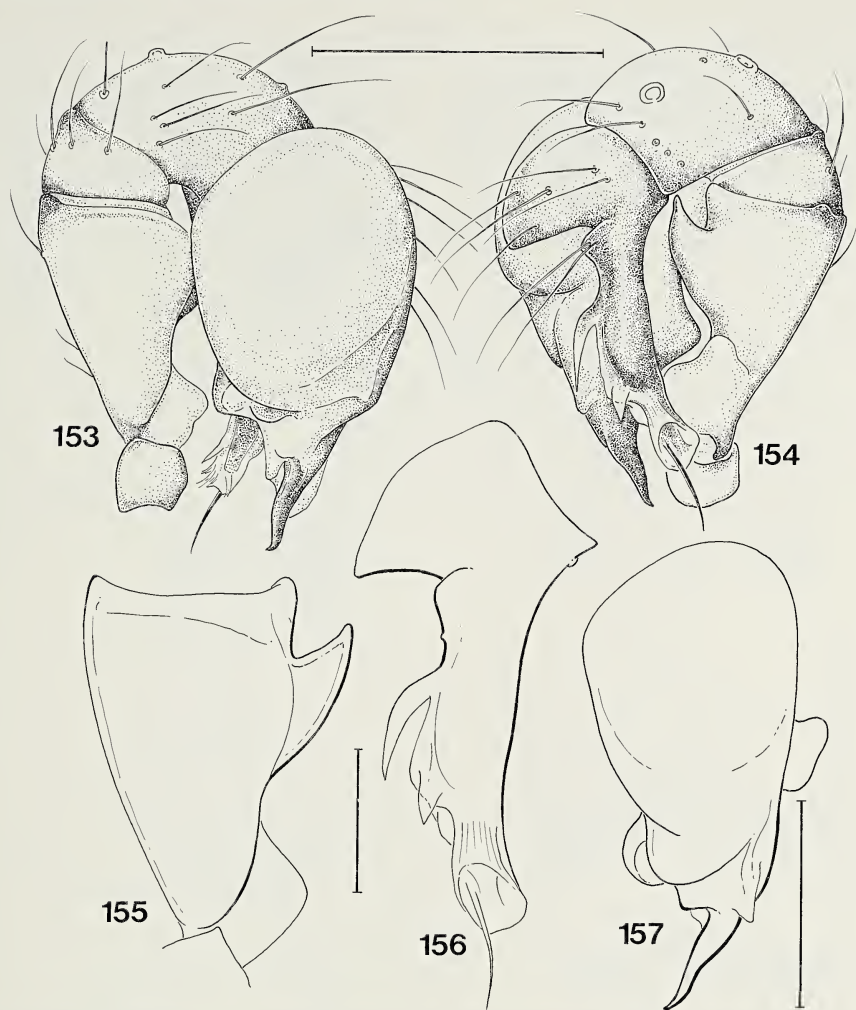
Figures 153–157.—*Modisimus dilutus* Gertsch, left male pedipalp. 153, Prolateral view; 154, Retrolateral view; 155, Femur, prolateral view; 156, Procursus, retrolateral view; 157, Bulb, dorso-prolateral view. Scale bars = 0.3 mm (153, 154); 0.1 mm (155, 156); 0.2 mm (157).

terior side of eye turret. Sternum and clypeus ochre-brown. Opisthosoma dorsally greenish-ochre with black spots, similar to *M. guatuso* new species (Fig. 61), ventrally lighter, with brown genital plate, another brown spot anterior to spinnerets, and black stripe in between. Legs ochre-brown with slightly darker rings on femora (distally) and tibiae (proximally and distally). Six eyes on eye turret, procursus, bulb, and femur apophysis as in Figs. 128–131, chelicerae with one patch of modified hairs on each side (Fig. 132), legs without spines. *Measurements:* Total length: 3.0, prosoma length: 1.0, width: 1.1, opisthosoma length: 2.0; leg 1: fem: 8.8, pat: 0.6, tib: 8.6, met: 17.0, tar: 2.6, total: 37.6, tibind: 71; leg 2 missing, leg 3: 18.9, leg 4: 21.2.

Female holotype: Colors mostly as in male, with orange-ochre sternum, brown epigynum with a pair of characteristic black denticles (Figs. 133, 134), back stripe behind epigynum. *Measurements:* Total length: 3.6, prosoma length: 1.0, width: 1.2, opisthosoma length: 2.6; leg 1: fem: 7.6, pat: 0.5, tib: 7.3, met: 13.3, tar: 2.2, total: 30.8, tibind: 57; leg 2 partly missing, leg 3: 15.6, leg 4: 18.0. *Tibia 1 from female paratype:* 7.2.

Other material examined.—1♀ from Rara Avis, Prov. Heredia, Costa Rica, elev. 540–700 m, July 1996 (R.L. Rodriguez).
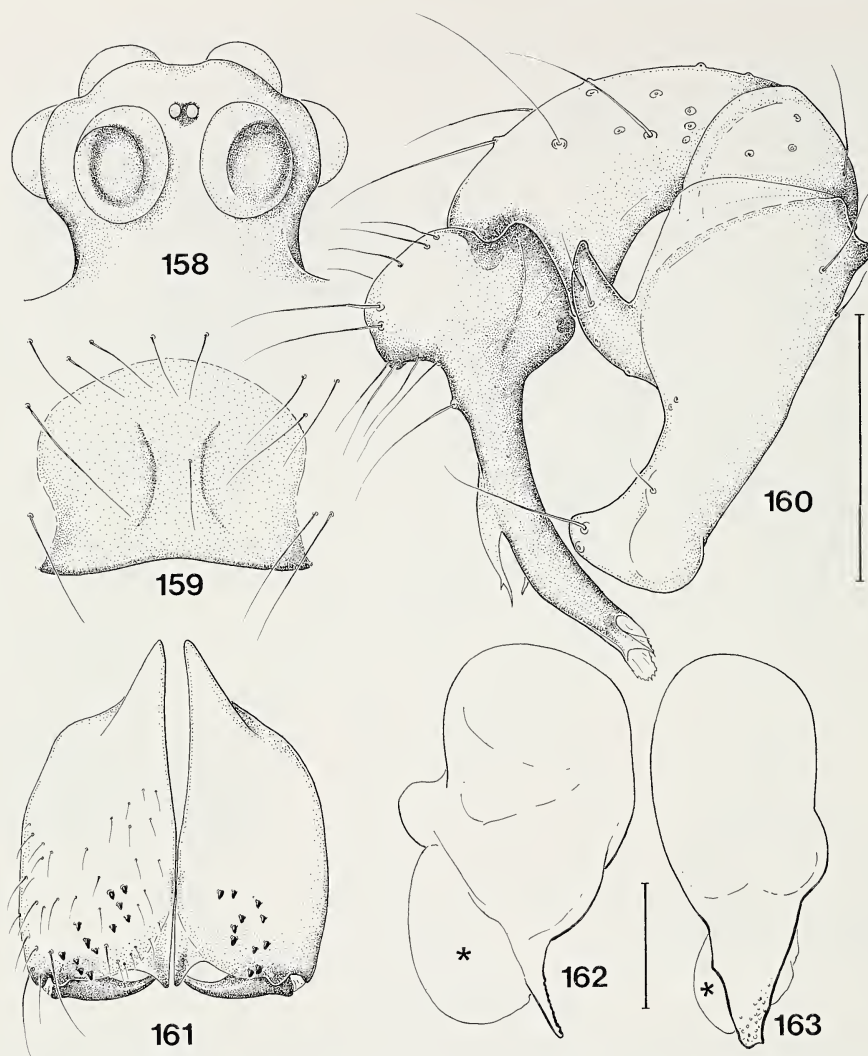
Figures 158–163.—*Modisimus inornatus* Cambridge. 158. Eye turret of female with tiny anterior median eyes; 159, Epigynum, ventral view; 160, Left male pedipalp, retrolateral view (bulb missing); 161, Male chelicerae, frontal view; 162, Left bulb, retrolateral view (asterisk: sperm mass?); 163, Left bulb, ventral view (asterisk: sperm mass?). Scale bars = 0.3 mm (160); 0.2 mm (162, 163).

Distribution.—Known only from the two mentioned localities in Prov. Heredia, Costa Rica.

Modisimus selvanegra new species
(Figs. 135–142)

Type data.—Male holotype and female paratype from La Selva Negra, a forest about 12 km N Matagalpa, Dept. Matagalpa, Nicaragua, elev. about 1300 m, from dome shaped webs near the ground, mostly under dead leaves, 24 July 1995 (B.A. Huber) (UCR).

Etymology.—Specific name from type locality.

Diagnosis.—Dark small species with characteristic shape of male pedipalpal procursus (Figs. 137, 138), and characteristically formed spines on male chelicerae (Fig. 141).

Description.—*Male:* Carapace ochre-brown, with darker median stripe, clypeus colored as carapace, sternum ochre-yellow with two darker longitudinal stripes. Pedipalps and chelicerae ochre-brown. Legs ochre-brown, with hardly visible darker rings on femora (distally) and tibiae (proximally and distally). Opisthosoma dorsally greenish-gray with black spots, some small white spots disap-
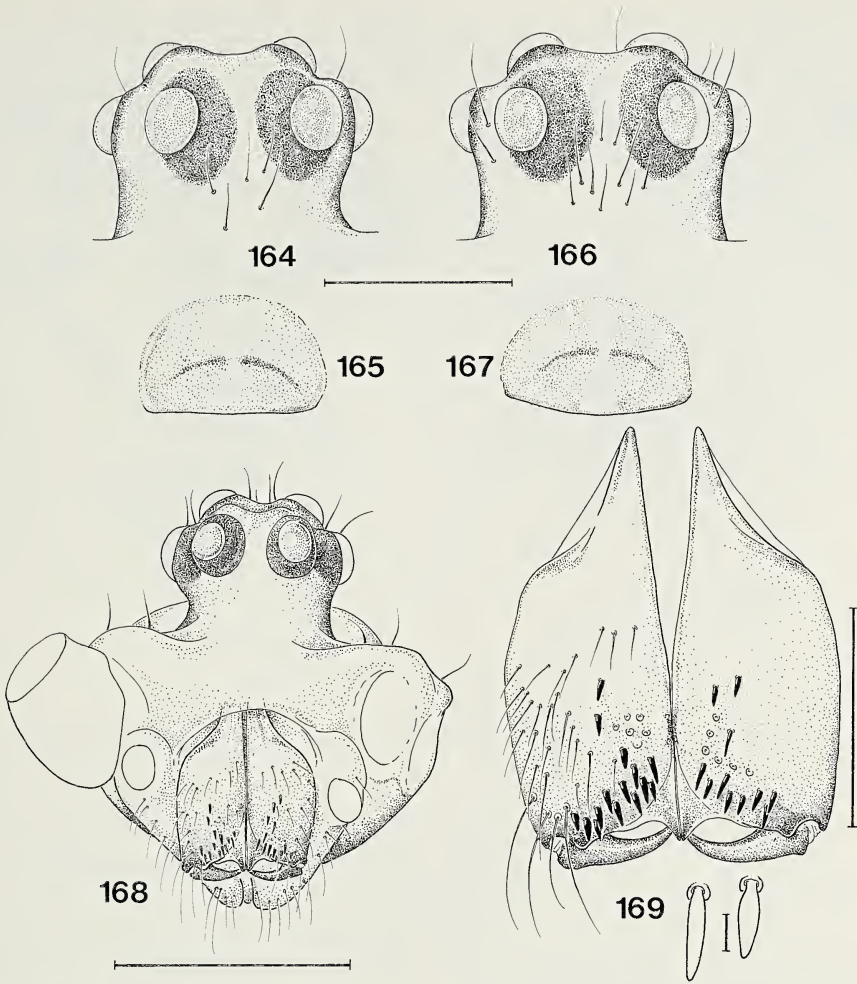
Figures 164–169. Species of *Modisimus*. 164–167. *Modisimus maculatipes* Cambridge. 164, Type of *M. maculatipes*, eye turret, frontal view; 165, Type of *M. maculatipes*, epigynum, ventral view; 166, Type of *M. putus* Cambridge, new synonymy, eye turret, frontal view; 167, Type of *M. putus* new synonymy, epigynum, ventral view. 168, *Modisimus propinquus* Cambridge, male prosoma, frontal view; 169, *Modisimus propinquus* Cambridge, chelicerae, frontal view, with two modified hairs enlarged. Scale bars = 0.2 mm (164–167, 169); 0.5 mm (168); 0.01 mm (modified hairs).

peared rapidly in most specimens, ventrally with brown genital plate, black stripe behind it and smaller brownish spot before spinnerets. Six eyes on eye turret, pedipalp as shown in Figs. 136–140, chelicerae with one patch of characteristically formed modified hairs on each side (Fig. 141 - only some individuals have the single distal modified hair). Legs without spines. *Measurements of male holotype:* Total length: 2.8, prosoma length: 1.0, width: 1.1, opisthosoma length: 1.8; leg 1: fem: 7.0, pat: 0.4, tib: 6.8, met: 11.9, tar: 1.9,

total: 28.0, tibind: 61; leg 2: 17.3, leg 3: 11.8, leg 4: 14.8.

Female: Colors mostly as in male, sternum darker with lighter spot in middle, epigynum brown, as shown in Fig. 142, with a short black stripe behind it. Dark rings on legs more pronounced than in male. *Measurements of female paratype:* Total length: 2.2, prosoma length: 0.7, width: 0.9, opisthosoma length: 1.5; leg 1: fem: 4.0, pat: 0.3, tib: 4.1, met: 6.7, tar: 1.4, total: 16.5, tibind: 48; leg 2: 10.6, leg 3: 7.8, leg 4: 9.9.
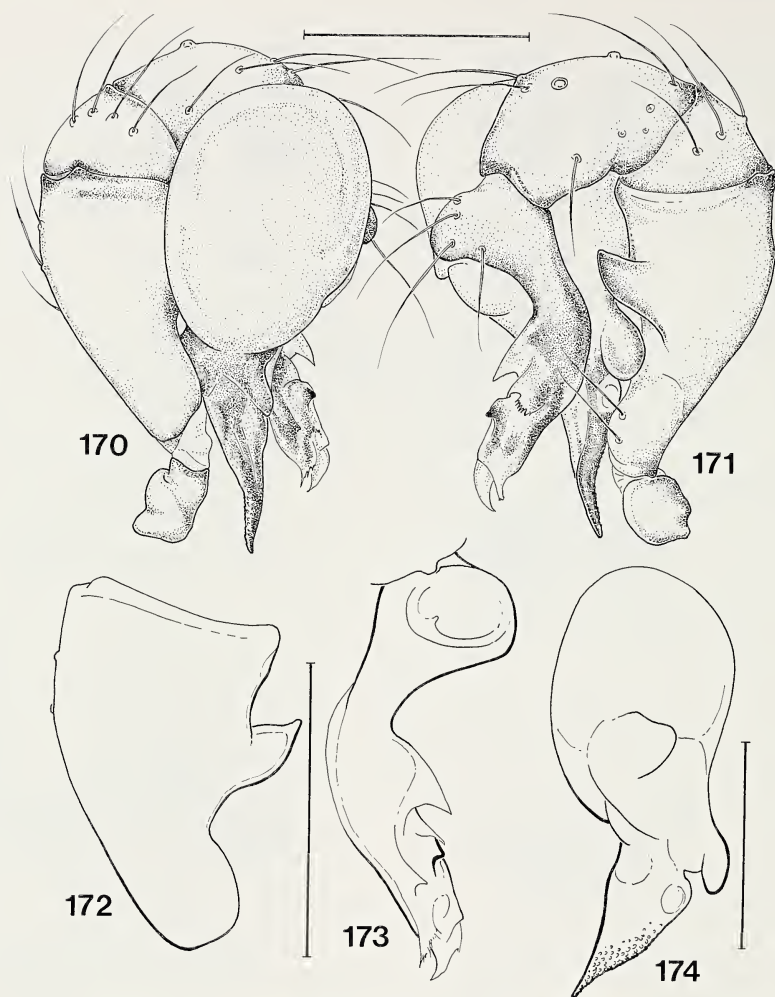
Figures 170–174.—*Modisimus propinquus* Cambridge, left male pedipalp. 170, Prolateral view; 171, Retrolateral view; 172, Femur; 173, Procursus, prolateral view; 174, Bulb, ventral view. Scale bars = 0.3 mm.

Tibia 1 in other material: 17♂: 5.7–6.9 (x̄ = 6.3); 12♀: 3.6–4.3 (x̄ = 3.9).

Other material examined.—18♂13♀ from type locality, same collection data as types.

Distribution.—Known only from type locality.

Modisimus tortuguero new species
(Figs. 143–148)

Type data.—Male holotype and female paratype from forest at Cerro Tortuguero (6 km NNW Tortuguero village), Prov. Limón, Costa Rica, at sea level, close to the ground in humid, shaded places, 8 August 1996 (B.A. Huber) (UCR).

Etymology.—Specific name from type locality.

Diagnosis.—Dark species closely related to *M. guatuso* and *M. cahuita*, distinguished from first by high numbers of spines (about 40) in two rows on the male femur 1 (*M. guatuso* has up to about 15 spines on femur 1), from second by flat epigynum (Fig. 148 - *M. cahuita* has a pair of protuberances on the epigynum: Figs. 34, 35).

Description.—*Male:* Carapace ochre-brown, darker on posterior side of eye turret, clypeus colored as carapace, pedipalps and chelicerae brown, sternum brown with ochre lateral margins and median stripe. Legs ochre-brown, with slightly darker rings on femora
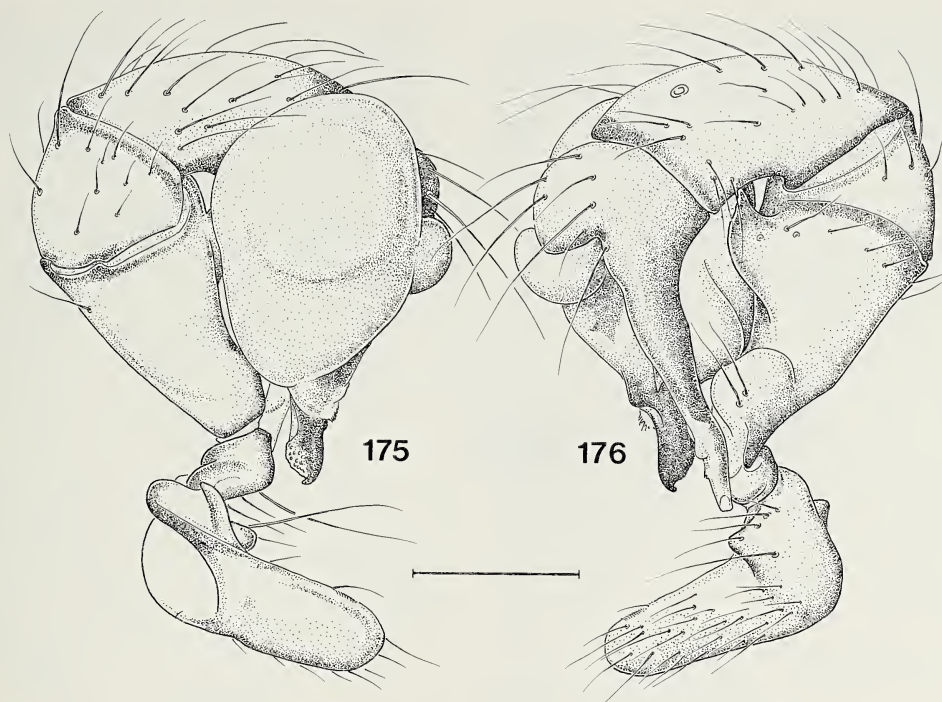
Figures 175, 176.—*Modisimus pulchellus* Banks, left male pedipalp. 175, Prolateral view; 176, Retrolateral view. Scale bar = 0.3 mm.

(distally) and tibiae (proximally and distally). Opisthosoma greenish-gray, covered dorsally with large black and smaller white spots in the same pattern as *M. guatuso* new species (Fig. 61), ventrally with brown genital plate, black stripe behind it and another dark spot before spinnerets. Six eyes on eye turret, genitalia not distinguishable from those of *M. guatuso* new species, except maybe by the stronger dorsal spine on the procursus (arrow in Fig. 143). Bulbs and femur apophysis as in Figs. 144–146. Chelicerae with one patch of modified hairs on each side (Fig. 147). Femora 1 and 2 (sometimes also 3) with two rows of spines ventrally (about 40 on femur 1). *Measurements of male holotype:* Total length: 3.3, prosoma length: 1.1, width: 1.3, opisthosoma length: 2.2; leg 1: fem: 7.3, pat: 0.5, tib: 7.5, met: 13.3, tar: 2.0, total: 30.6, tibind: 60; leg 2: 19.4, leg 3: 14.6, leg 4: 16.7.

Female: Colors as in male, but sternum lighter, opisthosoma ventrally only with black stripe behind brown epigynum (Fig. 148). Legs without spines. *Measurements of female paratype:* Total length: 2.9, prosoma length: 1.1, width: 1.1, opisthosoma length: 1.8; leg 1: fem: 6.5, pat: 0.4, tib: 6.4, met: 11.9, tar:

2.5, total: 28.0, tibind: 64; leg 2: 17.6, leg 3: 13.6, leg 4: 16.2.

Tibia 1 in 9 other males: 6.6–8.0 ($\bar{x}$ = 7.4).

Other material examined.—9♂ from type locality, same collection data as types. Tortuguero (not further specified), 1♂, 4–5 February 1982 (C.E. Valerio) (UCR).

Distribution.—Known only from Tortuguero, Prov. Limón, Costa Rica.

Modisimus dilutus Gertsch 1941
(Figs. 149–157)

M. dilutus Gertsch 1941: 11–12, figs. 29–30; Nentwig 1993: 97.

Type data.—Male holotype, female paratype from Barro Colorado Island, Canal Zone, Panama, 14 & 18 July 1938 (E.G. Williams, Jr.) (AMNH), examined.

Diagnosis.—Small light species, distinguished from congeners by the procursus (Fig. 156) with its distal flagellum.

Redescription.—Gertsch's (1941) verbal description is detailed and accurate, but the drawings are insufficient and the leg measurements wrong. Procursus of distinctive shape
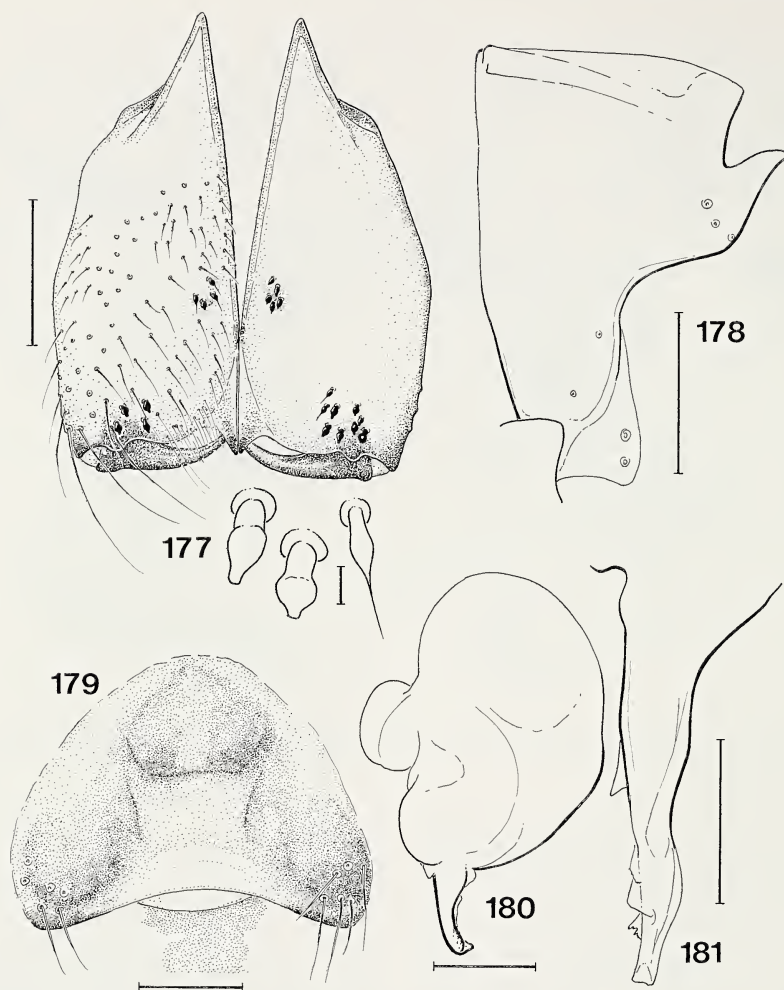
Figures 177–181.—*Modisimus pulchellus* Banks. 177, Male chelicerae, frontal view, with three modified hairs enlarged; 178, Male palpal femur; 179, Epigynum, ventral view; 180, Genital bulb, ventral view; 181, Left procursus, retrolateral view. Scale bars = 0.2 mm, 0.01 mm (modified hairs).

(Fig. 156), each chelicera set with one patch of modified hairs (Fig. 151). Prosoma and palps see Figs. 149–150, 153–157. Female epigynum as in Fig. 152. *Measurements of male holotype:* Prosoma length: 0.7, width: 0.7, opisthosoma damaged; leg 1 missing, leg 2: fem: 4.5, other segments missing; leg 3: 12.9, leg 4: 16.3.

Measurements of female paratype: Total length: 1.4, prosoma length: 0.5, width: 0.6, opisthosoma length: 0.9; leg 1: fem: 3.7, pat: 0.3, tib: 3.6, met: 5.5, tarsus missing, tibind: 75; leg 2 partly missing; leg 3: 6.8, leg 4: 8.7.

Distribution.—Known only from the Canal Zone, Panama.

Modisimus inornatus Cambridge 1895
(Figs. 158–163)

M. *inornatus* Cambridge 1895: 149, pl. 20, figs. 7, 7a-e; Cambridge 1899: 303, pl. 32, figs. 4, 4a-e; F. Cambridge 1902: 367, pl. 34, figs. 17, 17a-b, 18; Petrunkevitch 1925: 66; Gertsch & Davis 1937: 5; Reimoser 1939: 334; Gertsch & Davis 1942: 10.

M. *propinquus* Cambridge 1896: 223 (female only!), pl. 27, fig. 8f (misidentification).

Type data.—2♀ & 1♂, labeled as paratypes, from Teapa, Tabasco, Mexico, no date (H.H. Smith) (BMNH 1905. 4. 28. 1471–2), examined.

Diagnosis.—Medium-sized dark species,
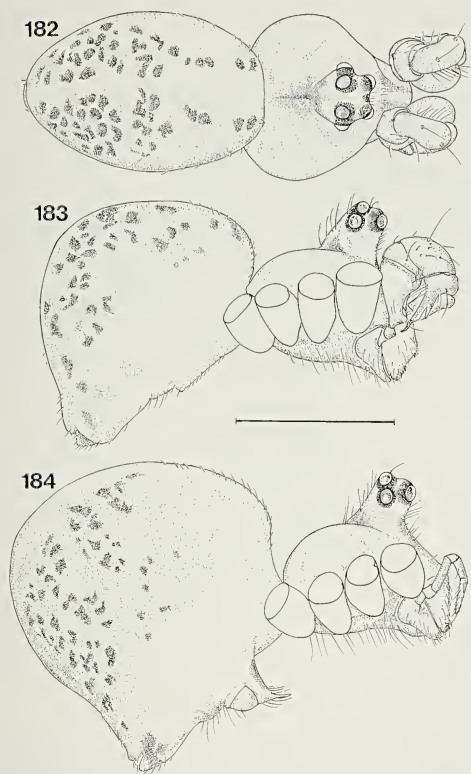
Figures 182–184.—*Modisimus texanus* Banks. 182, Male, dorsal view; 183, Male, lateral view; 184, Female, lateral view. Scale bar = 1 mm.

distinguished from the new species described in this paper by the procursus (Fig. 160: dorsal spine and additional, small spine more distally), and the shape of the femur apophysis (Fig. 160). Epigynum flat and simple (Fig. 159).

Redescription.—*Male:* Apart from the good original verbal description, it must be noted that the large bulge at the bulb (asterisks in Figs. 162, 163) may be an accidental accretion, maybe sperm. The spines on the male chelicerae are short (Fig. 161), procursus and femur apophysis as in Fig. 160. *Measurements:* Total length: 2.7, prosoma length: 1.1, width: 1.0, opisthosoma length: 1.6, legs missing or unmeasurable.

Female: Epigynum as in Fig. 159; the opisthosoma of one female is dorsally covered with small dark spots, in the other one it is unicolored. In one of the females, the AMEs are present (Fig. 158); they are lacking in the other female and in the male. *Measurements of 'female 1':* Total length: 2.5, prosoma length: 0.7, width: 0.9, opisthosoma length:

1.8; femur 1: 5.0. *Measurements of 'female 2':* Total length: 2.5, prosoma length: 0.8, width: 0.8, opisthosoma length: 1.7; femur 1: 4.0. *Measurements of female that accompanies holotype of M. propinquus:* Total length: 2.2, prosoma length: 0.8, width: 0.8; opisthosoma length: 1.4; femur 1: 4.3.

Other material examined.—One female from type locality, same collection data, together with the male holotype of *M. propinquus* (BMNH).

Distribution.—Most records are from Mexico (Tabasco, San Luis Potosí, Tamaulipas) (Cambridge 1895, 1896, 1899; Gertsch & Davis 1937, 1942). The species was also reported from Costa Rica (Reimoser 1939) and Panama (Petrunkevitch 1925). These authors probably did not compare their specimens with the types and provided no drawings. Moreover, the species is not present in any of the collections studied by the author. I have not seen Reimoser's and Petrunkevitch's material, but consider it probable that their identifications are wrong.

Modisimus maculatipes Cambridge 1895 (Figs. 164–167)

M. maculatipes Cambridge 1895: 148, pl. 20, figs. 5, 5a-e; F. Cambridge 1902: 367, pl. 34, fig. 20; Banks 1929: 56; Gertsch & Davis 1942: 10; Nentwig 1993: 98.

M. putus Cambridge, 1895: 148, pl. 20, figs. 6, 6a-e; F. Cambridge 1902: 368, pl. 34, fig. 21; Chickering 1936: 452. (NEW SYNONYMY).

Type data.—*M. maculatipes:* female labeled as lectotype, from Teapa, Tabasco, Mexico, no date (H.H. Smith) (BMNH 1905. 4. 28. 1473–4–part), examined. *M. putus:* female holotype from Teapa, Tabasco, Mexico, no date (H.H. Smith) (BMNH), examined.

Diagnosis.—Small dark species, with simple, flat epigynum (Figs. 165,167). Distinguished from the new species described in the present paper by the size and shape of the epigynum.

Redescription.—*Female:* Both specimens are now ochre-yellow, the opisthosoma lacks the pattern from the original description (Cambridge 1895) which is detailed and needs no repetition. The eye turrets and epigyna are practically identical in both specimens (Figs. 164–167). *Measurements of M. maculatipes, female:* Total length: 1.9, prosoma length: 0.7, width: 0.7, opisthosoma length: 1.2; leg 1:
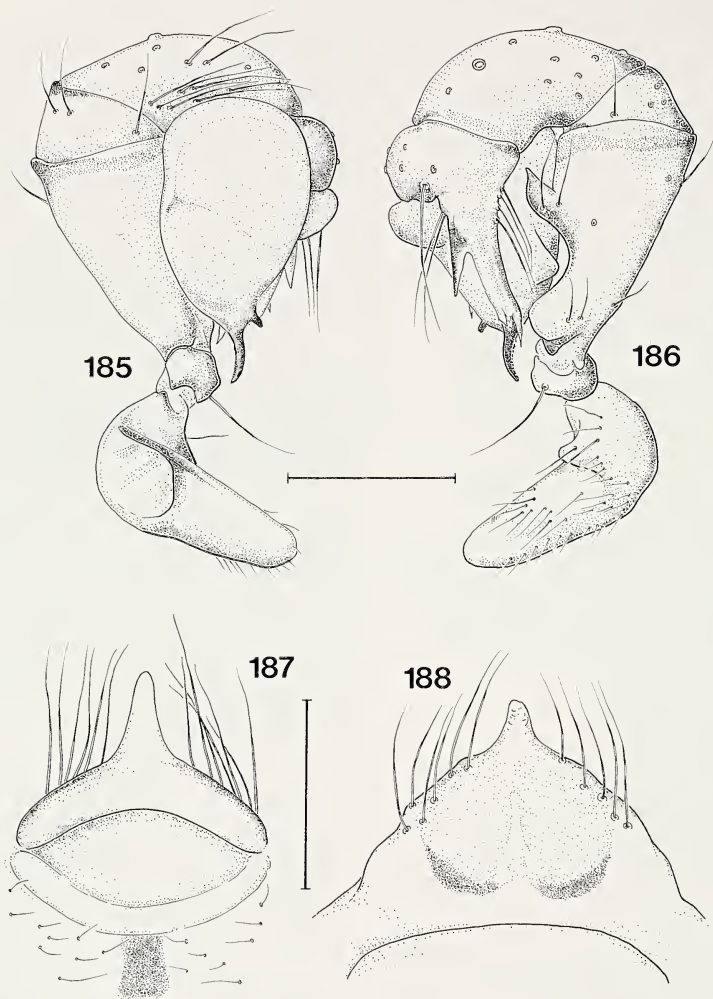
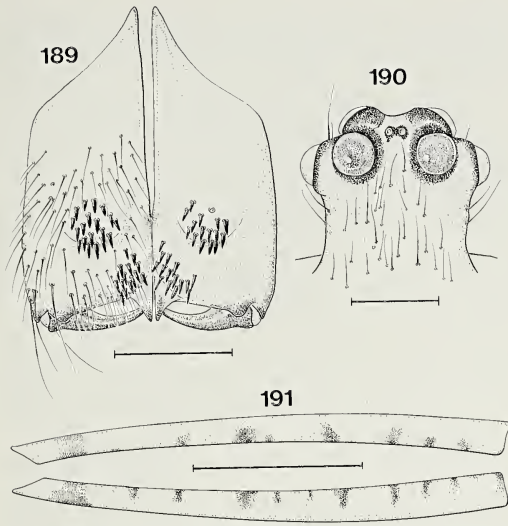Figures 185–188.—*Modisimus texanus* Banks. 185, Left male pedipalp, prolateral view; 186, Left male pedipalp, retrolateral view; 187, Epigynum, ventro-posterior view; 188, Epigynum, frontal view. Scale bars = 0.3 mm.

fem: 3.2, pat: 0.3, tib: 3.1, met: 5.1, tar: 1.1, total: 12.8, tibind: 33; leg 2: 7.9, leg 3: 5.9, leg 4: 7.6. *Measurements of M. putus, female:* Total length: 2.2, prosoma length: 0.7, width: 0.8, opisthosoma length: 1.5; leg 1: fem: 3.6, pat: 0.3, tib: 3.6, met: 5.8, tar: 1.2, total: 14.4, tibind: 45; leg 2: 8.5, leg 3: 6.5, leg 4: 8.4.

Justification of synonymy.—Cambridge (1895) noted that *M. putus* "closely resembles *M. maculatipes* in all essential characters". The differences were as follows: the latter was paler, had "some indistinct white spots" on the opisthosoma, the rings on the legs were almost absent, the "genital aperture" was larger and more prominent, and the tarsal ar-

ticulations seemed to be more distinct. None of these characters is appropriate to separate two species: recently molted individuals tend to be paler and to have the rings on the legs less distinct; white spots on the opisthosoma often disappear rapidly in ethanol; and the epigynum is not larger in *M. putus* (Fig. 167), and probably appeared more prominent because of a plug (which is now absent). The eye pattern, often used by previous authors to separate species, is practically identical in the two specimens (Figs. 164, 166). Both specimens are labeled with "Teapa 167" and might even have been collected together.

Distribution.—*M. maculatipes* has been

Figures 189–191.—*Modisimus texanus* Banks. 189, Male chelicerae, frontal view; 190, Eye turret, frontal view; 191, Female femur 3 in both lateral views. Scale bars = 0.2 mm (189, 190), 1 mm (191).

recorded from Mexico (Tabasco and Veracruz) (Cambridge 1895; Gertsch & Davis 1942), and from Panama (Canal Zone) (Banks 1929; Nentwig 1993). The two latter authors provided no drawings, and did probably not examine the type. *M. putus* has also been recorded from Mexico (Tabasco) (Cambridge 1895), and from Panama (Canal Zone) (Chickering 1936). Again, Chickering provided no drawings. Since the species is apparently absent in the large Costa Rican collections studied, it should be regarded as known only from Mexico, and the Panamanian records probably result from misidentifications.

Modisimus propinquus Cambridge 1896
(Figs. 168–174)

M. propinquus Cambridge 1896: 223 (only male!; female see *M. inornatus*), pl. 27, figs. 8, 8a-e; F. Cambridge 1902: 367, pl. 34, figs. 19, 19a-b; Gertsch 1973: 149; Brignoli 1973: 217–218; Nentwig 1993: 98.

Type data.—Male holotype from Teapa, Tabasco, Mexico, no date (H.H. Smith) (BMNH), examined. The male is accompanied by a female *M. inornatus* in a second subvial.

Diagnosis.—Small dark species, distinguished from congeners by the bent procursus with an apophysis distal to the dorsal spine

(Figs. 171, 173), and by the bulb with a globular projection near the bulbal apophysis (Figs. 171, 174).

Redescription.—*Male holotype:* The original verbal description is very precise and needs no repetition. Eye turret relatively high (Fig. 168). For details on chelicerae and pedipalps see Figs. 169–174. *Measurements:* Total length: 1.8, prosoma length: 0.6, width: 0.8, opisthosoma length: 1.2; all legs missing.

Distribution.—The species has been reported from Mexico (Tabasco, Chiapas) (Cambridge 1896; Gertsch 1973; Brignoli 1973) and Panama (Canal Zone) (Nentwig 1993). The latter author did probably not compare his specimens with the type, and provided no illustrations. Moreover, the species is absent in the large Costa Rican collections studied by the author, supporting the idea that Nentwig's (1993) Panamanian material may have been misidentified.

Modisimus pulchellus Banks 1929
(Figs. 175–181)

M. pulchellus Banks 1929: 56–57, figs. 16, 21, 68. Nentwig 1993: 98.

Type data.—6♂3♀ & 7juv syntypes from Barro Colorado Island, Canal Zone, Panama, 18–29 July 1928(?), and August 1928(?) (N. Banks) (MCZ), examined.

Diagnosis.—Large dark species, similar in some respects to the Costa Rican *M. dominical* new species, but with triangular epigynum (Fig. 179) and with small dorsal spine on procursus which does not end in two tips (Fig. 181).

Redescription.—*Male:* Habitus essentially as in *M. guatuso* new species (Fig. 61). Carapace ochre-brown, eye turret slightly darker, clypeus without marking, sternum yellowish-brown, darker anteriorly. Legs ochre-brown with dark rings distally on femora and tibiae. Opisthosoma dorsally pale greenish-gray with dark spots (in same pattern as *M. guatuso* new species - Fig. 61), ventrally with short dark stripe behind brown genital plate. Six eyes on eye turret, pedipalps as in Figs. 175–176, with distinctive procursus (Fig. 181). Femur apophysis and bulb as in Figs. 178, 180. Chelicerae with two patches of distinctively shaped hairs (Fig. 177), femora 1 and 2 with one row of spines ventrally. *Measurements of a male syntype:* (from vial labeled "July 18–29") Total length: 3.5, prosoma length: 1.2, width: 1.4,

opisthosoma length: 2.3; leg 1: fem: 7.8, pat: 0.5, tib: 7.8, met: 13.2, tar: 2.2, total: 31.5, tibind: 61; leg 2: 20.7, leg 3 missing, leg 4: 20.6.

Female: Habitus and colors as in male, with large distinctive epigynum (Fig. 179). *Measurements of a female in MCZ:* (collected by A.M. Chickering in 1934): Total length: 2.8, prosoma length: 1.0, width: 1.1, opisthosoma length: 1.8; leg 1: fem: 5.4, pat: 0.4, tib: 5.2, other segments missing, tibind: 55; leg 2: 13.8, leg 3: 11.7, leg 4: 14.1.

Tibia 1 in other material: 2♂: 7.9, 8.6; 4♀: 4.8, 5.3, 5.5, 5.6.

Other material examined.—3♂8♀ & 4juv from type locality, 16 June–7 October 1934 (A.M. Chickering) (MCZ). 2♀ & 2juv from Forest Preserve, Canal Zone, 14 February 1954 (A.M. Chickering) (MCZ).

Distribution.—Known only from the Canal Zone, Panama.

Modisimus texanus Banks 1906
(Figs. 182–191)

M. texanus Banks 1906: 94. Comstock 1912: 327; fig. 319. Gertsch & Davis 1937: 4. Gertsch & Mulaik 1941: 321. Gertsch & Davis 1942: 10. Gertsch 1973: 149.

Type data.—Female holotype from Austin (Texas, USA), March (no year), (J.H. Comstock) (MCZ), examined.

Diagnosis.—Dark eight-eyed species, easily distinguished from all known congeners by the epigynum with its long median projection (Figs. 184, 187–188), and by the dark half-rings ventrally on the femora (Fig. 191).

Redescription.—*Male:* Carapace ochre, darker medially, clypeus with a pair of dark stripes down to chelicerae (Fig. 182), sternum ochre with darker bands laterally. Legs ochre with characteristic darker half-rings and rings on femora (Fig. 191), patella also dark, tibiae with only two rings each (one proximally, one distally). Opisthosoma greenish-gray with dark spots dorsally (Figs. 182, 183), ventrally dark spot between genital plate and spinnerets. Eight eyes on high eye turret (Fig. 190), pedipalps as shown in Figs. 185–186, chelicerae with two patches of modified hairs on each side (Fig. 189), legs without spines. *Measurements of male from Reseca:* (5 mi SE Brownsville, Texas - AMNH). Total length: 2.5, prosoma length: 1.0, width: 1.0, opisthosoma

length: 1.5; leg 1: fem: 5.9, pat: 0.4, tib: 6.2, met: 9.3, tar: 1.4, total: 23.2, tibind: 50; leg 2: 15.0, leg 3: 12.2, leg 4: 14.1.

Female: Colors as in male, in some specimens there are some gray spots visible on the opisthosoma which were probably white in the live spiders (Fig. 184). Epigynum of characteristic shape (Figs. 184, 187, 188), anterior side brown, posterior side pale ochre; legs without spines. *Measurements of female from Reseca:* (AMNH). Total length: 2.8, prosoma length: 1.1, width: 1.0, opisthosoma length: 1.7; leg 1: fem: 5.1, pat: 0.4, tib: 5.2, met: 8.0, tar: 1.2, total: 19.9, tibind: 43; leg 2: 12.5, leg 3: 9.9, leg 4: 12.4.

Measurements of other material: Female holotype: prosoma width: 1.1, fem 1: 4.3. Other material from AMNH: *Tibia 1 in* 10♂: 4.9–8.2 (x̄ = 6.8); 15♀: 3.3–6.3 (x̄ = 4.5).

Other material examined.—(All in AMNH). USA. *Texas:* Rio Grande City, 1♀ & 2 juv, July 1934 (S. Mulaik). Llano County, 1♀ & 1juv, 10–12 July 1936 (L.I. Davis). Reseca, 5 mi SE Brownsville, 2♂1♀, 26 September 1937 (L.I. Davis & M. Fones). Edinburg, 1♂1♀, September-December 1933 (S. Mulaik), 2♂8♀ & 6juv, 15–25 May 1935 (S. Mulaik), 3♂1♀, 10 June 1935 (S. Mulaik). Driscoll, 1♀, 23 March 1936 (S. Mulaik). Arroyo Salado, Zapato County, 2♀, 9 February 1935 (S. Mulaik). 19 mi S Kerrville, 1♂, 23 May 1939 (S. Mulaik). Palm Grove, Brownsville, 1♀, 30 May 1939 (S. Mulaik). Cameron County, 1♀, September 1936 (L.I. Davis). 5 mi E Rio Grande City, 1♂, 1 May 1937 (S. Mulaik). Laredo, 2♂3♀, 9 February 1935 (S. Mulaik). La Gringa Reseca, Cameron County, 2♂1♀, 19 September 1937 (L.I. Davis). Brazos River, 5 mi W Hearne, 1♀, July 1938 (L.I. Davis). **MEXICO.** *Nuevo Leon:* 28 mi N Monterrey, 1♂1♀, 7 July 1936 (L.I. Davis).

Distribution.—Known from Texas (USA) and north-eastern Mexico (Nuevo Leon, Tamaulipas, San Luis Potosí).

ACKNOWLEDGMENTS

LITERATURE CITED

Banks, N. 1906. Description of new American spiders. Proc. Entomol. Soc. Washington, 7:94–101.

Banks, N. 1929. Spiders from Panama. Bull. Mus. Comp. Zool., 69:51–96.

Briceño, R.D. 1985. Sticky balls in webs of the spider *Modisimus* sp. (Araneae, Pholcidae). J. Arachnol., 13:267–269.

Brignoli, P.M. 1973. Notes on spiders, mainly cave dwelling, of Southern Mexico and Guatemala (Araneae). Accad. Naz. Lincei, 171:195–238.

Bryant, E.B. 1940. Cuban spiders in the Museum of Comparative Zoology. Bull. Mus. Comp. Zool., 86:247–532.

Bryant, E.B. 1948. The spiders of Hispaniola. Bull. Mus. Comp. Zool., 100:329–447.

Cambridge, O.P. 1889–1902. Arachnida - Araneidea, Vol. 1. *In* Biologia Centrali-Americana.

Cambridge, F.O.P. 1897–1905. Arachnida, Araneida and Opiliones, Vol. 2. *In* Biologia Centrali-Americana.

Chickering, A.M. 1936. Additions to the list of known species of spiders from Barro Colorado Island, Panama. Trans. American Microsc. Soc., 55:449–456.

Comstock, J.H. 1912. The Spider Book. Doubleday, Page & Company.

Deeleman-Reinhold, C.L. 1986. Leaf-dwelling Pholcidae in Indo-Australian rain forests. 9th Internat. Congr. Arachnol. (Panama, 1983):45–48.

Eberhard, W.G. 1992. Web construction by *Modisimus* sp. (Araneae, Pholcidae). J. Arachnol., 20:25–34.

Eberhard, W.G. & R.D. Briceño. 1983. Chivalry in pholcid spiders. Behav. Ecol. Sociobiol., 13:189–195.

Eberhard, W.G. & R.D. Briceño. 1985. Behavior and ecology of four species of *Modisimus* and *Blechroscelis* (Araneae, Pholcidae). Rev. Arachnol., 6:29–36.

Foelix, R.F. & I-Wu Chu-Wang. 1973. The morphology of spider sensilla. II. Chemoreceptors. Tissue & Cell, 5:461–478.

Gertsch, W.J. 1941. Report on some arachnids from Barro Colorado Island, Canal Zone. American Mus. Nov., 1146:1–14.

Gertsch, W.J. 1971. A report on some Mexican cave spiders. Mexican Cave Stud. Bull., 4:47–111.

Gertsch, W.J. 1973. A report on cave spiders from Mexico and Central America. Mexican Cave Stud. Bull., 5:141–163.

Gertsch, W.J. & L.I. Davis. 1937. Report on a collection of spiders from Mexico. I. American Mus. Nov., 961:1–29.

Gertsch, W.J. & L.I. Davis. 1942. Report on a collection of spiders from Mexico. IV. American Mus. Nov., 1158:1–19.

Gertsch, W.J. & S. Mulaik. 1941. The spiders of Texas I. Bull. American Mus. Nat. Hist., 77:307–340.

Gertsch, W.J. & S.B. Peck. 1992. The pholcid spiders of the Galápagos Islands, Ecuador (Araneae: Pholcidae). Canadian. J. Zool., 70:1185–1199.

Helversen, O. von. 1976. Gedanken zur Evolution der Paarungsstellung bei den Spinnen (Arachnida: Araneae). Entomol. Germanica, 3(1/2):13–28.

Huber, B.A. 1994. Genital morphology, copulatory mechanism and reproductive biology in *Psilochorus simoni* (Berland, 1911) (Pholcidae; Araneae). Netherlands J. Zool., 44(1–2):85–99.

Huber, B.A. 1996. On the distinction between *Modisimus* and *Hedypsilus* (Pholcidae; Araneae), with notes on behaviour and natural history. Zool. Scr., 25:233–240.

Huber, B.A. 1997. On American "*Micromerys*" and *Metagonia* (Pholcidae, Araneae), with notes on natural history and genital mechanics. Zool. Scr., 25(4):341–363.

Huber, B.A. in press a. On the "valve" in the genitalia of female pholcids (Pholcidae, Araneae). Bull. British Arachnol. Soc.

Huber, B.A. in press b. Genital mechanics in some neotropical spiders (Araneae: Pholcidae), with implications for systematics. J. Zool., London.

Huber, B.A. & W.G. Eberhard. 1994. Courtship, copulation and genital mechanics in *Physocyclus globosus* (Araneae, Pholcidae). Canadian J. Zool., 75(6):905–908.

Mello-Leitão, C. de. 1946. Notas sobre os Filistatidae e Pholcidae. An. Acad. Brasileira Cienc., 18:39–83.

Nentwig, W. 1993. Spiders of Panama. Flora & Fauna Handbook, # 12. Sandhill Crane Press, Inc., Gainesville, Florida. 274 pp.

Petrunkevitch, A. 1925. Arachnida from Panama. Trans. Connecticut Acad. Arts Sci., 27:51–248.

Petrunkevitch, A. 1929. The spiders of Porto Rico. Trans. Connecticut Acad. Arts Sci., 30:1–158.

Platnick, N.I., J.A. Coddington, R.R. Forster & C.E. Griswold. 1991. Spinneret morphology and the phylogeny of haplogyne spiders (Araneae, Araneomorphae). American Mus. Nov., 3016:1–73.

Reimoser, E. 1939. Wissenschaftliche Ergebnisse der österreichischen biologischen Expedition nach Costa Rica. Ann. Naturhist. Mus. Wien, 50:328–386.

Simon, E. 1893a. Descriptions d'espèces et de genres nouveaux de l'ordre des Araneae. Ann. Soc. Ent. France, 62:299–330.

Simon, E. 1893b. Histoire Naturelle des Araignées. 2e edit, 1:456–487. Paris.

Uhl, G. 1993. Sperm storage and repeated egg pro-

duction in female *Pholcus phalangioides* Fuess-
lin (Araneae). Bull. Soc. Neuchâteloise Sci. Nat.,
116:245–252.

Uhl, G. 1994. Genital morphology and sperm stor-
age in *Pholcus phalangioides* (Fuesslin, 1775)
(Pholcidae; Araneae). Acta Zool. (Stockholm),
75:1–12.

Uhl, G., B.A. Huber & W. Rose. 1995. Male ped-

ipalp morphology and copulatory mechanism in
Pholcus phalangioides (Fuesslin, 1775) (Pholci-
dae, Araneae). Bull. British Arachnol. Soc., 10:
1–9.

Zuñiga, V.C.M. 1980. Lista anotada de especies de
arañas de Costa Rica. Brenesia, 18:301–351.

PREDATION ON SOCIAL AND SOLITARY INDIVIDUALS OF THE SPIDER *STEGODYPHUS DUMICOLA* (ARANEAE, ERESIDAE)

Johannes R. Henschel: Desert Ecological Research Unit of Namibia, P.O. Box 1592, Swakopmund, Namibia

ABSTRACT.   Encounters and effects of predators were examined for group-living and solitary dispersers of the spider *Stegodyphus dumicola* Pocock 1898 (family Eresidae) in Namibia. Birds and araneophagous spiders were major predators of solitary spiders; group members living in large, tough, complex nests were less vulnerable. Arboreal pugnacious ants *Anoplolepis steingroeveri* (Forel 1894) frequently attacked *S. dumicola* colonies of all sizes. As a means of defense against ants, the spiders produced copious amounts of sticky cribellar silk. Solitary spiders were incapable of sustaining this resistance for as long as groups could and usually died when ants attacked. Solitary individuals were, however, less likely to contract a contagious fungal disease that spread in large, old nests after rain. I conclude that the action of predators may explain why *S. dumicola* tend to be avidly social as well as prudently solitary.

Group living has behavioral, ecological and genetic consequences for spiders (Buskirk 1981; Rypstra 1993; Avilés 1993, 1996). The fundamental ecological reasons why some spiders spend their entire lives in groups may differ in different species. Safety from predators is often invoked as an explanation for grouping in animals (Inman & Krebs 1987). The encounter effect predicts that individuals encounter predators at a lower rate, due to foraging constraints by the predators. Once an encounter occurs, the dilution effect predicts that a member's probability of being captured decreases with group size.

Groups of non-territorial permanently-social spiders (hereafter referred to as social spiders) may have the possibility to lower their predation risk by using large, complex, communal retreats that provide physical protection. Cooperative defense is another possibility. The potential for cooperation is one of the distinguishing characteristics of social spiders (Avilés 1996), but its manifestations are not well-known. The suggested increased safety via communal fortification (Seibt & Wickler 1988a) and defense has not been confirmed.

Here I examine how *Stegodyphus dumicola* Pocock 1898 (Eresidae), living in groups or solitarily (Le Roy 1979; Seibt & Wickler 1988a; Henschel 1993), are affected by various kinds of predators (Meikle 1986; Seibt & Wickler 1988a; Griswold & Meikle 1990). In

particular, I examined the roles of the silk and of defense in providing protection.

Stegodyphus dumicola occupy nests that are attached to tree branches at heights of 0.5–1.5 m. Cribellar sheet webs extend from the nests in different directions. Nest entrances point downwards and the tops are sealed. Colonies of *S. dumicola* are polydomous, i.e., different nests are interconnected with one web, or monodomous, i.e., having isolated nests, including founder colonies of solitary dispersing females. Generations are annual and the secondary sex-ratio is female-biased (12% males on average; Henschel, Lubin & Schneider 1995a). In Namibia, females mature from January onwards (mid-summer), produce eggs during February and March, care for offspring during March and April, and die during April to June when they are consumed by gerontophagous juveniles (Seibt & Wickler 1987). Most solitary dispersal by females occurs during January to March. Males mature in mid-summer, but are short-lived and apparently mate within the parent colony (Henschel et al. 1995a). Males that emigrate do not establish new nests, but perhaps join solitary females. The current study concentrates on females.

I examined (a) the predator encounter rates, vulnerability, and survival of *S. dumicola* individuals and colonies, and (b) the responses and anti-predator measures of *S. dumicola* towards each predator. These factors are dis-

cussed in terms of risk-related attributes of group-living and solitary dispersal by *S. dumicola*.

METHODS

Study area.—Most field work was conducted on the farm Christirina (23°25'S, 18°00'E), 170 km SE of Windhoek in Namibia, on the periphery of the Kalahari Desert. *Stegodyphus dumicola* were abundant (>100 nests per hectare) in an area of 20 × 20 km of moderately dense dwarf *Acacia* woodland surrounding Christirina. Intensive monitoring was carried out in an area of 35 × 45 m (referred to as the Windpump) that contained 122 trees. This area was surrounded by several hectares where all nests were marked and incidental observations and measurements were made (referred to as Christirina). Some field work was also conducted on farms near Christirina (Beenbreck, Nauas and Uhlenhorst), Windhoek (22°35'S, 17°05'E), Etendeka Mountain Camp (19°50'S, 14°00'E) and Hobatere Lodge (19°16'S, 14°25'E). The interior of Namibia is semi-arid with rainfalls being sporadic. The average summer rainfall recorded at Christirina is 250 mm, but in the dry summers of 1991/2 and 1992/3, less than 150 mm fell only late in the season.

Procedures.—Christirina was visited 15 times during the mid to late summer seasons, January-May, of 1991–1993 at approximately monthly intervals for a total duration of 40 days. Data are based on these monthly spot checks of colonies and systematic observations were not conducted.

Many spiders were adult during the monitoring seasons. Group size was determined either directly by coercing spiders from small nests, or by applying the mark-recapture technique using the Lincoln index (Southwood 1978; the median of three counts for each colony correlates with known group size: $r^2 =$ 0.90; n = 6; deviating by 4.7 ±SD 16.4% above actual counts). I marked 938 spiders; some of these served to identify the origin of new colonies.

Spider predators were identified by their presence at spider nests or by the type of damage. Indirect signs included tearing of nests by birds and the disappearance of *S. dumicola* that coincided with the appearance of araneophagous spiders at the *S. dumicola* nest. Wasp parasitoid attacks were recognized by the fact that paralyzed spiders were positioned by the wasp near the nest entrance (Ward & Henschel 1992). The history of an ant attack was revealed by the presence of numerous ant carcasses in the nest lining. Occasionally, direct observations of predation by all of these species were made, which confirmed their status as predators. Fungus was recorded as a cause of death when spiders became lethargic and died in nests overgrown with fungal hyphae. Detectability of predator signs may differ, as birds that snatch spiders outside the nest leave no conclusive signs, and signs of ant attacks disappear when the surviving spiders cover them with silk. Some of the foreign spiders could have been "boarders" and may not necessarily have been responsible for the disappearance of *S. dumicola*. In 53% of all cases, the cause of *S. dumicola* colony extinction could not be ascertained. These are excluded from the analyses.

The survival of dispersing spiders was tested by artificial relocation. Spiders ($n = 497$) were taken out of their nests and allowed to build new retreats in the laboratory in groups of 30 ($n = 10$), 5 (n = 21), 2 ($n = 20$) and 1 ($n = 52$). At night these were attached to different *S. dumicola*-free trees in the typical locations and positions of natural nests. All nests in a 100 m radius were monitored at monthly intervals to ascertain the survival of experimental spiders at the release site or elsewhere. Dispersal >100 m is not expected (Henschel et al. 1995b) and spiders that disappeared were assumed to be dead.

Stegodyphus dumicola that disappeared at the Windpump site were assumed to be dead if they could not be relocated nor traced by inference to new nests within a 100 m radius in all directions. All nests were marked in a 1 ha area surrounding the Windpump site; all new nests were easily detected and marked. Marked *S. dumicola* were observed to disperse over distances that were much shorter than the radius of the area monitored (Henschel, Schneider & Lubin 1995b). Therefore it is highly likely that disappearances were due to mortality. Furthermore, there was no evidence of individuals crossing among colonies except between interconnected polydomous nests. Movement between colonies is considered unlikely, as social spiders are highly inbred (Smith & Engel 1994; Avilés 1996; for *S. dumicola*: Wickler & Seibt 1993) and

Table 1.—Number of colonies, number of individuals in groups and solitary, and mean group size ±SD of *Stegodyphus dumicola* at Windpump at the beginning of three breeding seasons (1991–1993). Old groups were those that persisted from the previous generation, including group-living offspring of solitary females.

	1991	1992	1993	Total
Number of colonies (individuals)				
Old groups	9 (134)	20 (613)	2 (55)	31 (802)
New groups	45 (372)	4 (108)	0 (0)	49 (480)
Solitary	159 (159)	6 (6)	26 (26)	191 (191)
Total	213 (665)	30 (727)	28 (81)	271 (1473)
Mean group size (±SD)				
Old groups	14.9 ± 13.0	30.6 ± 28.1	27.5 ± 3.5	25.9 ± 24.5
New groups	8.3 ± 13.5	27.0 ± 16.5	0.0 ± 0.0	9.8 ± 14.5
Solitary	1.0	1.0	1.0	1.0
Total	3.1 ± 7.7	24.2 ± 26.2	2.9 ± 7.0	5.4 ± 13.0

group size did not increase, except by reproduction.

In nine populations, all nests were counted, solitary individuals were counted and signs of ant attack were recorded. The populations were: Christirina in 1991, 1992 & 1993 (n = 213, 70 & 198 nests), Uhlenhorst (n = 48), Hobatere (n = 100), Windhoek (n = 31), Nauas (n = 20), Etendeka (n = 12) and Beenbrek (n = 54). Voucher specimens are deposited at the National Museum of Namibia in Windhoek. Means are given ± 1 SD; confidence limits were 95%, unless otherwise indicated.

RESULTS

Population.—The number of colonies and individuals present at Windpump varied among years by up to an order of magnitude (Table 1). New colonies were formed in each breeding season, mostly by solitary females, which, on average, comprised 13% of the population. This proportion differed between years (χ^2 = 148.8; df = 2; P < 0.001) and was strongly reduced in 1992 (0.8%). New colonies were larger in 1992 than they were in 1991 (Mann-Whitney U = 24; P = 0.016), although in both years, old and new colonies did not differ significantly from each other (U-test; P > 0.06). Average colony size (including solitary spiders) was larger in 1992 than in 1991 (U = 259.5; P < 0.001). The 1993 population did not differ significantly from previous years in the above parameters.

Mortalities.—Colony extinction rate was high at Windpump (89% of 271 colonies in three years). Table 2 documents only the final causes of extinction of colonies at Windpump. For a founder iniv/idual, one mortality event resulted in extinction of that colony, whereas a larger group only went extinct after several mortality events, of which only the final event is shown in Table 2. In spite of this, the overall survival rates between breeding seasons of solitary individuals and groups did not differ significantly (χ^2 = 0.28; df = 1; P = 0.59). Table 3 shows the proportion of all encounters with predators observed for solitary-living and group-living individuals during the course of fieldwork at Christirina. Both measures of mortality, colony extinctions at Windpump (Table 2) and observed encounters of predators by *S. dumicola* individuals at Christirina (Table 3), are analyzed for each predator below.

Ants.—Ground-nesting diurnal ants *Anoplolepis steingroeveri* (Forel 1894) frequently encountered *S. dumicola* because both species had an affinity for trees. The spiders built their retreats against branches; the ants crawled up the branches to tend scale insects and aphids (Homoptera: Coccina and Aphididae) and repelled other fauna. When I checked all 122 trees at Windpump during one afternoon in February 1992, *A. steingroeveri* were present on every tree, of which 18 also contained *S. dumicola* nests. It is therefore not surprising that ants frequently encountered spider nests. Sometimes, the ants attacked *S. dumicola* by

Table 2.—Rate and cause of colony extinction of *Stegodyphus dumicola* at Windpump during three breeding seasons (1991–1993).

	1991	1992	1993	Total
Colony extinctions				
Groups	44/54	22/24	0/2	66/80
Solitary	149/159	6/6	20/26	175/191
Group extinctions				
Ants	1/44	17/22	0/0	18/66
Birds	0/44	0/22	0/0	0/66
Spiders	7/44	0/22	0/0	7/66
Other & unknown	36/44	5/22	0/0	41/66
Solitary extinctions				
Ants	13/149	6/6	3/20	22/175
Birds	24/149	0/6	10/20	34/175
Spiders	29/149	0/6	2/20	31/175
Other & unknown	83/149	0/6	5/20	88/175

gathering in large numbers (100s to 1000s) and invading the spider nests. At Christirina in 1992, about 5% of the spider nests ($n = 70$) were under attack by ants at any given time of observation. Over the season, 60% of the nests were attacked. The ants could continue attacks for several consecutive days and nests could be attacked repeatedly days or months later.

Ants dismembered the remains of spider prey, tore open cocoons to remove spider eggs, killed some spiders in the nest and killed those that dropped to the ground. Bites by only a few of these 1–2 mg ants killed even a 100–200 mg female. The ants transported their booty into their nest in the ground.

Ant raids on colonies reduced spider group size. Spiders were counted in 11 colonies at Windpump in January, February and April 1992, yielding 22 records of group size changes. In the intervals between the monthly

Table 3.—Signs of encounters of various predators by groups and solitary individuals of *Stegodyphus dumicola* at Christirina made during the course of fieldwork (percent for columns).

Predator	Group	Solitary
Ants	79.3	28.5
Spiders	4.0	33.8
Birds	2.9	33.8
Wasps	8.0	2.6
Fungus	5.7	1.3
n	174	151

monitoring, ants raided the colonies 16 times. Ant-raided colonies declined by 57% ± 20, significantly more than the 15% ± 15 by those not raided (ANCOVA: $F = 17.7$, $P = 0.0005$; variable: final colony size; covariate: initial colony size; treatment: ant raid/no raid; there was no significant interaction between the treatment and the covariate: $F = 0.13$, $P = 0.7$). I estimated that if the ants appropriated all losses from ant-raided spider colonies, they would gain *ca.* 0.3–17 g of spiders as prey per raid.

Ants could decimate *S. dumicola* populations. The 1992/3 cohort of spiders at the Windpump started with 20 colonies. Repeated ant attacks on spiders reduced them until only two colonies (10%) survived into the next breeding season. At another site within the same population, 54 colonies in one patch succumbed in a similar way resulting in the local extinction of the patch. By contrast, all 11 colonies survived in two other patches not frequented by ants.

The response of *S. dumicola* to *A. steingroeveri* was based on deterrence and evasion and never on counterattack (e.g., biting). The initial approach of single ants to the nest was prevented by sticky bands of cribellar silk (22.7 ± 8.4 mm wide; range 10–45) that the spiders laid around branches below the nest. These cribellar bands were laid only in three ant-frequented areas and were not present in four other areas where ant attacks were rare (< 10% of the colonies were attacked). None-

theless, ants could cross the cribellar bands by swarming over each other. The spiders then left the nest, taking some egg cocoons with them. They positioned themselves below the nest in a portico of loosely-woven wide tunnels with porous walls bearing much cribellar silk. There they spun more layers of cribellar silk. Group members took turns in spinning at the ant front. This fresh silk hindered pursuit and many ants became permanently entangled. If ants continued swarming towards the spiders when they stopped spinning, the spiders then moved onto the capture web or dropped to the ground, where they were sometimes overcome by other *A. steingroeveri*.

Spiders did not escape to other branches or trees during ant raids. In polydomous colonies they abandoned nests that were under ant attack in favor of other connected nests. While ant raids took place, many *A. steingroeveri* were also active on surrounding trees, which could make the establishment of new nests difficult for spiders at such times.

Most of the predator encounters observed at spider groups were by ants, whereas other predators gained in relative importance for solitary individuals (Table 3; $\chi^2 = 84.7$, $df = 1$, $P < 0.001$). However, some individuals survived an ant raid in 85% of 20 groups at Christirina whereas all 28 solitary individuals died when ants attacked ($\chi^2 = 13.1$, $df = 1$, $P < 0.05$). Many groups even survived several ant attacks, although the extinction rate increased from 15% with the first attack on a colony to 24, 46 and 43% with the second, third and fourth attacks respectively. Four of 20 groups survived four attacks. Protection may be enhanced in polydomous colonies. At Christirina, a group of small *Acacia* trees that was festooned with webs of a polydomous colony comprising twelve nests, was free of ants throughout the study period, although ants frequented nearby *Acacia* trees.

The rate of solitary emigration by *S. dumicola* had an inverse relationship to the frequency of ant attacks. In nine populations, the proportion of nests with solitary individuals was negatively correlated to the extent of ant attack (Fig. 1) ($R_s = -0.78$; $P < 0.05$).

Araneophagous spiders.—Clubionidae, Gnaphosidae, Heteropodidae: *Olios* sp., Tetragnathidae: *Nephila senegalensis* (Walckenaer 1841), Salticidae, Thomisidae (listed by relative frequency) were implicated as preda-
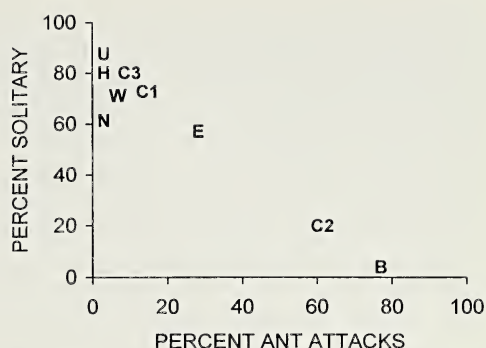

Figure 1.—Occurrence of solitary dispersal of *Stegodyphus dumicola* in populations that differed in the proportion of nests attacked by ants. Populations are Christirina in 1991 (C1), 1992 (C2) & 1993 (C3), Uhlenhorst (U), Hobatere (H), Windhoek (W), Nauas (N), Etendeka (E) and Beenbrek (B).

tors of *S. dumicola*. All of these, except *N. senegalensis*, entered the nests. *Nephila senegalensis* attached its orb-web to the nest of *S. dumicola* and seized spiders that came to the attachment site.

Stegodyphus dumicola did not appear to employ specific countermeasures against araneophagous spiders. They were either passive (towards Clubionidae, Thomisidae and Salticidae), attracted towards them (*N. senegalensis*), or helpless against them (Heteropodidae and Gnaphosidae).

Araneophagous spiders attacked mainly solitary-living or emigrating *S. dumicola* (Tables 2, 3). For example, as members of a domestic *S. dumicola* colony emigrated singly, they were seized by pholcid spiders *Smeringopus* sp. ($n = 11$) that surrounded but did not enter the social colony. Only eight non-emigrant *S. dumicola* survived out of a colony of 180 spiders. This suggests that the predation risk to solitary emigrant *S. dumicola* was not communicated to the parent colony.

Birds.—Any of the 30 insectivorous birds occurring at Windpump could have been predators of *S. dumicola*. Nine species were seen at spider nests. During ant raids, spiders could not retreat when birds approached. Gabar goshawks (*Micronisus gabar*) carried large *S. dumicola* nests onto their own nests in high trees ($n = 8$ colonies); however, goshawks are not regarded as true predators, although they removed spiders from the local population (see Henschel et al. 1992a,b).

During the heat of the day, *S. dumicola* sitting in the cool shade below the nest quickly retreated into the nest upon the approach of birds, often leaving their egg cocoons behind. After some minutes, they re-emerged cautiously. The location of nests against branches provided birds with convenient perches from which to attack *S. dumicola* nests. The nests of larger groupings, however, are made of tough multiple layers of silk, making it difficult for birds to extract the spiders. By contrast, birds were capable of tearing small nests of solitary spiders apart to extract the spiders.

Wasps.—Pompilid wasps *Pseudopompilus funereus* (Arnold 1932) lured *S. dumicola* out from the nest onto the web where they were captured and then positioned below the nest, as described for *S. lineatus* (Latreille 1817) by Ward & Henschel (1992). The spiders may mistake wasps for potential prey. Observations at Christirina, pooled with other data, showed that individual rates of wasp parasitism did not differ for groups and solitary individuals (Henschel et al. 1996).

Fungus.—Entire colonies of *S. dumicola* could die when unidentified fungi spread through wet nests. Inhaled spores appear to be harmful also to humans (pers. obs.). Exposed nests dried quickly in the sun, evidently preventing the growth of fungus. However, during two wet periods of several days each, 12 colonies at Christirina succumbed to fungus. None were affected during long dry spells or after brief rainstorms. At Windpump, all but 7 of 249 nests were exposed to the sun for at least several hours on typically sunny summer days. The relative susceptibility of spiders from the seven shaded nests to outbreaks of fungus could not be tested in the field, as all of these colonies died from causes other than fungus (ants, spiders, unknown) before the rains came. Fungus began to proliferate on large, wet nests ($n = 21$) that were taken indoors and did not dry within 1–2 days. Several spiders died before I removed others from the infested nests. By contrast, fungus did not grow in any of the 126 dry nests taken indoors for examination.

Large, spongy nests of groups appeared to retain water for longer than the single tunnels of solitary spiders, which may explain the higher susceptibility of fungal outbreaks in groups (Table 3).

Dispersal of *S. dumicola*.—Risk during

Table 4.—Attributes of dispersal behavior of *Stegodyphus dumicola* that may enhance survival (+) when various predators are enountered.

Dispersal	Ant	Spider	Bird	Wasp	Fungus
Leave natal colony	−	−	−	−	+
Emigrate at night	+	−	+	?	−
Short distance	+	+	−	−	−
Bridging lines	+	+	−	−	−
Group dispersal	+	+	+	−	−

dispersal was tested at Christirina by experimentally relocating 103 colonies of which 70% were solitary or pairs. A month later, all spiders had died in 94% of the nests, including all singles and pairs; another month later, the remaining spiders died. Spider groups survived significantly longer than singles or pairs (<1 month vs. >1 month: $\chi^2 = 14.8$, $df = 1$, $P < 0.05$). The final cause of extinction of all 103 colonies was known for 31 colonies: 77% were attacked by ants, 10% by other spiders, 6% by birds and 6% were dislodged and drowned in a storm.

Some behavioral attributes by naturally dispersing spiders may reduce the risk of predation (Table 4). By leaving the natal group, the spiders left old nests that often harbored lethal fungus. Spiders avoided encountering ants and birds away from their nest by dispersing at night, but may risk running into nocturnal wandering spiders (e.g., Heteropodidae). Short distances of dispersal should reduce the latter risk. Solitary emigrants typically did not move further than they could travel in an evening, and they established new nests by dawn (only 4 of 55 female dispersers were observed without nests). Dispersal distances were short (median = 4 m, quartiles = 3–8 m, $n = 17$). The maximum distance, 26 m, was much shorter than the area being monitored. None of the 938 spiders marked at Windpump appeared in the surrounding one hectare area, and there was no evidence that *S. dumicola* dispersed by ballooning (Henschel et al. 1995b; but see Wickler & Seibt 1986).

Dispersal was along bridging lines in all 48 cases where the method of dispersal could be established. Bridging lines enabled return to the parent colony if ants attacked; this was observed once, and the occurrence of inter-

connected empty nests was suggestive of similar attacks in at least a dozen cases. Bridging lines were in place for one day or longer; in 15% of the cases they were used by other colony members to form new groups.

DISCUSSION

The action of predators may explain why *S. dumicola* tend to be avidly social as well as prudently solitary. Risk of predation combines the effects of encounter rate with a predator and the spiders' vulnerability, which is affected by defense, nest impenetrability, avoidance and escape capabilities.

The poor defense of solitary individuals when faced with attacking ants made them highly vulnerable. By contrast, attacking ants had more difficulty penetrating colonies whose members kept them at bay by taking turns at spinning fresh silk. Araneophagous spiders could penetrate *S. dumicola* colonies of all sizes (see also Meikle 1986; Seibt & Wickler 1988a, 1988b; Wickler & Seibt 1988; Griswold & Meikle 1990), but groups may be less affected than solitary individuals, possibly due to the dilution effect or because emigrants were attacked more than residents. Birds other than the Gabar could more easily tear apart small nests of *S. dumicola* than large ones and could thus more easily capture solitary spiders than group members. Specialized pompilid wasps were potentially dangerous to all *S. dumicola* (Henschel et al. 1996), but their own populations were probably severely reduced by ants and birds preying on wasp larvae fixed beneath spider nests. The danger of fungus destroying colonies may grow with the age and size of the nests that accumulate spores. Furthermore, there could be a high risk of cross-infection among social group-members that frequently contact each other. During wet spells, groups of spiders in long-established nests may be in greater danger of contracting the disease than solitary spiders in new, small, clean nests.

There appear to be trade-offs for the spiders in reducing risk to specific predators. For example, nests in the sun build up heat loads in summer which may prevent fungal growth and deter ants and araneophagous spiders. However, sun-exposed nests also get too hot for *Stegodyphus* (Seibt & Wickler 1990; Henschel et al. 1992c), making it necessary for them to move out onto the web together with

their egg cocoons during hot hours. There, spiders and eggs may be more vulnerable to birds and wasps, including egg parasites (the latter were present, but were not examined).

Another trade-off involves nest size and group size. The very factors that may reduce the risk towards some predators increase the risk of *S. dumicola* contracting fungal disease. Many spiders are susceptible to common pathogenic fungi that do not appear to be species-specific (Nentwig 1985; Greenstone, Ignoffo & Samson 1987). It is possible that the risk of mycosis contracted from wet nests confines the distribution of *S. dumicola* to hot, sunny regions. In India, social *S. sarasinorum* Karsch 1891 seal the tops of their nests with thick layers of water-repellent silk that render nests rain-proof during the monsoon season (Bradoo 1972).

The ultimate ecological reasons for solitary dispersal have not been established. Dispersers reduce the static distribution pattern of colonies and may reach areas that are spared from catastrophes, such as outbreaks of fungal disease, escalating ant attacks, and, perhaps, major storms or fires. A more immediate reason for dispersal could be escaping intragroup competition for food, as has been suggested for *S. mimosarum* Pavesi 1883 (Ward & Enders 1985; Ward 1986; Seibt & Wickler 1988a). Surviving solitary females may have a higher reproductive output than they would have had if they had remained in groups (Wickler & Seibt 1993). Furthermore, their offspring grow up away from conspecific competitors. Henschel et al. (1995a) suggested that this may be how intermediate-sized, late-maturing female *S. dumicola* increase their fitness, as solitary emigrants that have removed their offspring from conspecific competitors may tend to have more fecund daughters than if they had not dispersed.

Increased overall safety from aggressive ants may be a reason for spiders not to disperse, though ants exert high direct and indirect tolls on *S. dumicola* of all group sizes. These include lost foraging time, greater exposure to birds, loss of eggs and of resources for their offspring, and, often, increased mortality. However, in addition to being predators, ants are cleaners in *S. dumicola* nests. They remove prey remains and kill parasitoid wasp larvae. In some other social spiders, ants appear to be exclusively scavengers/cleaners and

do not disturb the spiders (Furey & Riechert 1989; Downes 1994).

Stegodyphus dumicola protect themselves from ants by employing silk. They deter approaching ants with sticky cribellar bands wrapped around the nest-supporting branches and they defend themselves against attacking ants by constructing fresh cribellar-silk shields. These anti-predator measures are adjusted to the degree of threat, but exceed the capabilities of solitary spiders. For breeding Gabar goshawks, a potential benefit of translocating colonies of *S. dumicola* onto their own nests (Henschel et al. 1992a,b) would be keeping ants away from their chicks.

Escaping from attacking ants does not appear to be a solution for *S. dumicola* because ants also frequent the surrounding terrain. This is different for *S. sarasinorum* in India (Bradoo 1972); when attacked by ants, these spiders left and established new nests elsewhere. Though a new nest and web may incur a higher overall cost of silken material than the cost of a defensive shield, emigrating *S. sarasinorum* are not required to produce this at such a high rate as defenders would be.

Anoplolepis ants are widely distributed in southern Africa; and in the areas studied in central Namibia, they frequent most trees daily (Prins 1982). Other genera of arboreally-foraging ants that attack *S. dumicola* include *Acantholepis*, *Crematogaster* and *Pheidole* (Meikle 1986 pers. comm.; Seibt & Wickler 1988a; Le Roy pers. comm.; pers. obs.). These ants seek food in trees, particularly honeydew from scale insects and aphids, and repel other animals by chemical and physical means (Hölldobler & Wilson 1990). The frequent confrontations of *S. dumicola* with ants are a consequence of the spiders' reliance on retreats built against solid objects and their chosen microhabitat in tree branches.

By contrast, the sympatric solitary *S. bicolor* (O. Pickard-Cambridge 1869) builds its nest against stalks of grass and herbs that do not appear to be frequented by aggressive ants (pers. obs.). The ephemeral nature of these substrata in the presence of large ungulates may pose different problems for *S. bicolor* that occur at low densities of three or more orders of magnitude less than *S. dumicola*. Nevertheless, ants pose a potential problem for other species of solitary-living *Stegodyphus*. Schneider (1992) reports that ants an-

nually raided 3.6% of solitary *S. lineatus* in Greece. Although this is much less than the 23.2% incidence of wasp parasitism, the ability of ants to escalate their attacks would still appear to make them dangerous.

Arboreal ants may exert selective pressure on *S. dumicola* at the group level. All members of a colony under attack are affected. On the one hand, the actions of ants may restrict spider dispersal because ant encounters with groups provide potential emigrants a means to assess the danger of leaving the safety of the group. On the other hand, the ability of ants to eventually eliminate even the largest, resistant colonies, would place those spider demes with several dispersed sister/daughter colonies at a selective advantage. Dispersers that reach temporarily enemy-free sites can found new colonies that grow rapidly in the first few generations due to the high female productivity in small colonies (*sensu* Seibt & Wickler 1988a) and female-biased sex ratios (*sensu* Avilés 1993).

LITERATURE CITED

Avilés, L. 1993. Interdemic selection and the sex ratio: a social spider perspective. American Nat., 142:320–345.

Avilés, L. 1996. Causes and consequences of cooperation and permanent-sociality in spiders. Pp. 00–00, *In* Social competition and cooperation in insects and arachnids, Vol.2, Evolution of sociality. (B. Crespi & J. Choe, eds.). Princeton Univ. Press, Princeton, New Jersey.

Bradoo, R.L. 1972. Some observations on the ecology of the social spider *Stegodyphus sarasinorum* Karsch (Araneae: Eresidae) from India. Oriental Insects, 6:193–204.

Buskirk, R.E. 1981. Sociality in the Arachnida. Pp. 281–367, *In* Social insects, Vol. 2. (H.R. Hermann, ed.). Academic Press, New York.

Downes, M.F. 1994. Arthropod nest associates of the social spider *Phryganoporus candidus* (Ara-

neae: Desidae). Bull. British Arachnol. Soc., 9: 249–255.

Furey, R.E. & S.E. Riechert. 1989. *Agelena consociata* (Araneae, Agelenidae) and its nest associates: Insect cleaners. J. Arachnol., 17:240–242.

Greenstone, M.H., C.M. Ignoffo & R.A. Samson. 1987. Susceptibility of spider species to the fungus *Nomuraea atypicola*. J. Arachnol., 15:266–268.

Griswold, C.E. & T.C. Meikle. 1990. Social life in a web. Natural History, 3/90:6–10.

Henschel, J.R. 1993. Is solitary life an alternative for the social spider *Stegodyphus dumicola*? J. Namibian Sci. Soc., 43:71–79.

Henschel, J.R., Y.D. Lubin & J. Schneider. 1995a. Operational sex ratio and sexual competition in an inbreeding social spider, *Stegodyphus dumicola* (Araneae: Eresidae). Insectes Soc., 41:419–426.

Henschel, J.R., J. Mendelsohn & R. Simmons. 1992a. Is the association between the Gabar Goshawk and social spiders *Stegodyphus* mutualism or theft? Gabar, 6:57–59.

Henschel, J., J. Schneider & Y. Lubin. 1995b. Dispersal mechanisms by the spiders *Stegodyphus*: Do they balloon? J. Arachnol., 23:202–204.

Henschel, J.R., J. Schneider & T. Meikle. 1996. Does group-living or aggregation of the spiders *Stegodyphus* affect parasitism by pompilid wasps? Bull. British Arachnol. Soc., 10:138–140.

Henschel, J.R., R. Simmons & J. Mendelsohn. 1992b. Gabar goshawks and social spiders revisited: Untangling the web. Gabar, 7:49–50.

Henschel, J. R., D. Ward & Y. Lubin. 1992c. The importance of thermal factors for nest-site selection, web construction and behaviour of *Stegodyphus lineatus* (Araneae: Eresidae) in the Negev Desert. J. Therm. Biol., 17:97–106.

Hölldobler, B. & E.O. Wilson. 1990. The ants. Springer, Berlin.

Inman, A.J. & J. Krebs. 1987. Predation and group living. TREE, 2:31–32.

Le Roy, A. 1979. *Stegodyphus* observations. Spider Club News, 12:4–5.

Meikle, T. 1986. Nest associates of two species of group-living Eresidae in southern Africa. Pp. 275, *In* Actas X Congr. Intern. Arachnologia, Jaca, España. (J.A. Barrientos, ed.). Juvenil Press, Barcelona.

Nentwig, W. 1985. Parasitic fungi as a mortality factor of spiders. J. Arachnol., 13:272–274.

Prins, A.J. 1982. Review of *Anoplolepis* with reference to male genitalia, and notes on *Acropyga* (Hymenoptera, Formicidae). Ann. South African Mus., 89:215–247.

Rypstra, A.L. 1993. Prey size, social competition, and the development of reproductive division of labor in social spider groups. American Nat., 142:868–880.

Schneider, J. 1992. Die Wurzeln des Soziallebens bei der subsozialen Spinne *Stegodyphus lineatus* (Eresidae). Ph.D. dissertation, Ludwig-Maximilian-Universität, München, Germany.

Seibt, U. & W. Wickler. 1987. Gerontophagy versus cannibalism in the social spiders *Stegodyphus mimosarum* Pavesi and *Stegodyphus dumicola* Pocock. Anim. Behav., 35:1903–1904.

Seibt, U. & W. Wickler. 1988a. Bionomics and social structure of "Family Spider" of the genus *Stegodyphus*, with special reference to the African species *S. dumicola* and *S. mimosarum* (Araneida, Eresidae). Verh. naturwiss. Ver. Hamburg, 30:255–303.

Seibt, U. & W. Wickler. 1988b. Interspecific tolerance in social *Stegodyphus* spiders (Eresidae, Araneae). J. Arachnol., 16:35–39.

Seibt, U. & W. Wickler. 1990. The protective function of the compact silk nest of social *Stegodyphus* spiders (Araneae, Eresidae). Oecologia, 82: 317–321.

Smith, D.R. & M.S. Engel. 1994. Population structure in an Indian cooperative spider, *Stegodyphus sarasinorum* Karsch (Eresidae). J. Arachnol., 2: 108–113.

Southwood, T.R.E. 1978. Ecological methods with special reference to the study of insect populations, 2nd ed. Chapman & Hall, London.

Ward, D. & J.R. Henschel. 1992. Experimental evidence that a desert parasite keeps its host cool. Ethology, 92:135–142.

Ward, P.I. 1986. Prey availability increases less quickly than nest size in the social spider *Stegodyphus mimosarum*. Behaviour, 97:213–225.

Ward, P.I. & M.M. Enders. 1985. Conflict and cooperation in the group feeding of the social spider *Stegodyphus mimosarum*. Behaviour, 94: 167–182.

Wickler, W. & U. Seibt. 1986. Aerial dispersal by ballooning in adult *Stegodyphus mimosarum*. Naturwiss., 73:628–629.

Wickler, W. & U. Seibt. 1988. Two species of *Stegodyphus* spiders as solitary parasites in social *S. dumicola* colonies (Araneida, Eresidae). Verh. naturwiss. Ver. Hamburg, 30:311–317.

Wickler, W. & U. Seibt. 1993. Pedogenetic sociogenesis via the "sibling-route" and some consequences for *Stegodyphus* spiders. Ethology, 95: 1–18.

BEHAVIORAL ASYMMETRY IN RELATION TO BODY WEIGHT AND HUNGER IN THE TROPICAL SOCIAL SPIDER *ANELOSIMUS EXIMIUS* (ARANEAE, THERIDIIDAE)

Dieter Ebert[1]:   Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Republica de Panamá

ABSTRACT. It has been hypothesized that larger females of the social neotropical spider *Anelosimus eximius* (Keyserling 1884) (family Theridiidae) take advantage of the food captured by smaller females, and thus maintain a higher social rank within a colony. To test this hypothesis, the behavior of adult females in three colonies of *A. eximius* was observed in the Panama rain forest. Adult spiders with low body weights did most of the building, cleaning and repairing of the communal web, while heavier spiders more often took care of egg sacs. The latter stayed mostly inside safe retreats while low-weight spiders were mostly outside the retreats, where mortality was high. Reproducing spiders were of high body weight.

To test whether this behavioral asymmetry is related to the nutritional condition of a female a manipulation experiment was conducted. A comparison of adult females, which were either well fed or starved, showed that starved females do more web maintenance, spend more time outside the retreats and more often take part in attacking prey. I conclude that both hunger (recent feeding success) and general nutritional condition (body weight) are the cues for the observed behavioral asymmetry in colonies of *Anelosimus eximius*. It is currently unknown whether the observed asymmetry is stable over time or whether it is age-related.

Sociality in spiders provides an interesting and challenging parallel to its evolution in other social organisms, in particular social insects (Wilson 1971). Among spiders a wide continuum of sociality from temporal aggregation up to permanent social colonies is found (Buskirk 1981). Although morphological castes have never been observed (e.g., Lubin 1995), it was suggested that a dominance structure exists in colonies of *Anelosimus eximius* Simon, which supposedly leads to an asymmetrical distribution of behavior (Vollrath 1986a). Since fewer egg sacs than adult females are found within these colonies, and the rate of insemination of adult females is low, Vollrath (1986a) speculated that a few, larger females suppress smaller colony members. It has been shown that in *A. eximius* that particularly large prey items lead to feeding and reproductive asymmetries within colonies (Rypstra 1993). As a possible mechanism for this asymmetry, Vollrath (1986a) speculated that females take advantage of prey caught by smaller colony members. Thus, small spiders would conduct the dangerous task of prey cap-

ture while larger females reproduce. However, reproductive asymmetry could simply be due to the presence of some larger spiders which hunt more successfully, eat more prey and eventually gain enough resources to reproduce, while others are never able to reproduce. To understand whether reproductive asymmetry exists in natural colonies of *A. eximius* and, if so, how it is maintained, I investigated the behavior of adult *A. eximius* females in relation to spider size and hunger in three colonies in the Panama rain forest.

Colonies of the social spider *A. eximius* occur in neotropical rain forests from Panama to southern Brazil (Levi 1956, 1963) and are typically found in bushes or trees along roads, in forest gaps or in open habitat close to rain forests. Colonies may contain a few, or up to several thousand members, with overlapping generations (Christenson 1984; Vollrath 1986b, but see Avilés [1986] for possible exceptions) and cooperative care of brood (Vollrath & Rohde-Arndt 1983; Christenson 1984). The web consists of a basket-like sheet inside of which fallen leaves are used as retreats. Above the sheet is the snare, an irregular structure of non-sticky silk threads, which acts

[1]Current address: Institut für Zoology, Basel University, Rheinsprung 9, 4051 Basel, Switzerland.

to catch prey (see drawings in Vollrath [1982] and Christenson [1984]). Prey are attacked by one or several spiders and transported into a nearby retreat where feeding takes place. Communal attacks allow for capture of prey several times the size of adult spiders (Nentwig 1985; Rypstra 1990; Pasquet & Krafft 1992). Males rarely contribute in social activities. Sex ratio within colonies is strongly female biased (Avilés 1986; Vollrath 1986a) and as in other highly social spiders (Roeloffs & Riechert 1988), colonies are highly inbred (Vollrath 1982; Smith 1986). Both sexes are diploid (Vollrath 1986a).

Apart from prey capture and handling, colonies show a distinct bimodal daily activity pattern (Christenson 1984; Pasquet & Krafft 1992; D.E. pers. obs.). During both day and night hours most spiders stay motionless either close to or inside the retreats, although some females may feed spiderlings or clean egg sacs. Around sunrise and sunset, web maintenance activity (i.e., repair), cleaning and construction of snare and sheet, peaks for 1–2 hours.

METHODS

Anelosimus eximius colonies were found in Central Panama along El Llano-Carti Road, (2 miles south of Kuna Station, 78°57′W, 9°20′N), along a rainforest road close to the Atlantic coast (79°58′W, 9°25′N) and along the road to the highest elevation on Taboga Island (Pacific Ocean, off shore Panama City, 79°33′W, 8°47′N). Central Panama has a pronounced seasonality, with a dry season from December until May, during which insect abundance, and thus spider food, is lower than during the rainy season (Wolda 1978; Vollrath 1986a). My study was conducted from mid-December 1991 until mid-February 1992. On six days field work was interrupted by rain.

Observation of marked spiders was only possible by placing colonies into small isolated bushes, a treatment which seems not to affect the spiders' behavior (Vollrath & Rohde-Arndt 1983; Christenson 1984). Of nine colonies moved (with 15–25 adults and about 10–100 juveniles each), seven re-established new webs within the first night, while in two cases most spiders disappeared within the first night. Colonies were allowed to establish for one week. The new colonies had a diameter of 20–30 cm and the snare reached up to 60

cm in height. Natural colonies with similar numbers of females are in approximately the same size range (D.E. pers. obs.). In some cases I had to remove fallen leaves to allow free observation. Six of the seven colonies were used during the study. Experimental colonies were located in a tree gap along pipeline road (Parque Nacional Soberania, 79°45′W, 9°10′N) in a tropical lowland rainforest, an area suitable for *A. eximius* (Vollrath 1986b). All colonies were located within an area of 15 m diameter. No egg sacs were present in these colonies at the start of the study.

Estimation of nutritional conditions.— Cephalothorax width of 201 females from five natural colonies was measured to the nearest 0.01 mm using a dissecting microscope with ocular micrometer. The largest class of approximately normally distributed widths (1.27–1.59 mm) did not overlap with the size class of the penultimate instar (0.97–1.25 mm), allowing for reliable distinction between adult and sub-adult females.

In contrast to the cephalothorax, which is fixed by instar, the abdomen is distensible and increases in volume during feeding or egg production, allowing for assessment of nutritional condition without disturbing the spider (Anderson 1974; Foelix 1985). I classified abdomen-size of adult females according to classes from 1 to 9, where 1 represents the smallest (rod-shaped abdomen) and 9 represents the largest abdomen (egg-shaped). These classes were compared with body fresh-weight and cephalothorax width of 51 adult females.

Colony observation.—For 30 days three experimental colonies were observed for 2–8 successive hours per day (mean = 4.8 h/day), usually from early afternoon to 1800 h. Cumulative observation time was more than 100 h per colony. *A. eximius* shows two activity peaks per day, around sunrise and around sunset. Most observations on web maintenance activity are done around sunset, which might bias these data. However, on three occasions early in the study I observed spiders from 0600–0800 h and compared their activity with the evening activity. Since activity levels appeared not to differ between morning and evening observations, I studied web maintenance activity only in the evening.

All adult females were individually marked with a code of four non-toxic colors on ab-

domen and legs. These marking are perma-
nent, since adult spiders do not molt anymore.
At the beginning of the observation period
each day, I recorded the presence of adult fe-
males, females which had molted recently into
the adult stage, number of egg sacs, and the
length and number of prey carcasses. I further
classified abdomen-size of each adult female.
Bodies of dead females were removed from
colonies and cephalothorax width was mea-
sured.

At 10 minute intervals I recorded the lo-
cation (inside or outside retreat) and behavior
of every marked individual. Juveniles and
males were ignored. A female was considered
to be outside the retreat when her legs touched
the threads of the snare directly and she was
not located under a leaf. I distinguished the
following behaviors: web maintenance (repair,
cleaning and construction of snare and sheet),
care of egg sacs (guarding and cleaning of egg
sacs), feeding on prey and motionless waiting.
I estimated body length of prey in relation to
adult female body length (about 5 mm) and
noted the females which attacked, transported
and fed on the prey. Prey length and the
marked attacking females were also recorded
when prey escaped during attack. Although
prey length may be a poor predictor of prey
weight, (some prey may be short and fat,
whilst others are thin and long) over the whole
range of prey observed (about 1–25 mm) prey
length is likely to be a good predictor of
weight.

Food restriction experiment.—From ex-
perimental colonies 4, 5 and 6, I removed six
adult females each, marked and kept them in
two groups in 20 × 30 × 40 cm cages. One
cage was used for each treatment group and
each colony ($n = 6$). For one week, three fe-
males from each colony were starved while
the others were fed twice a day (around 0900
and 2000 h) with flies, wasps and grasshop-
pers caught around the colonies. To assign fe-
males to the starvation or feeding treatment I
caught them one by one and tossed a coin. All
cages were sprinkled with water twice a day.
All 18 spiders (3 colonies × 2 treatments ×
3 females) survived. After one week spiders
were placed back into their home colonies at
1800 h. The following three days I recorded
the behavior of these spiders in each colony
from 1200–1800 h.

Data analysis.—Data on spider location

(inside or outside retreat) were used only for
time periods between 0800–1700 h (inactive
period, Pasquet & Krafft 1992). Data on web
maintenance were used only between 1700–
1800 h (active period) because web mainte-
nance behavior was only observed during
hours of changing daylight and because spider
location and web maintenance were not in-
dependent (during web maintenance a spider
is always outside the retreat). The times for
egg care and web maintenance behavior, as
well as the time spent inside or outside the
retreats were calculated for each female as
proportion of the daily observation period. For
these calculations I did not consider times dur-
ing which at least one female was involved in
attacking or transporting prey and the first
hour of feeding on prey. Egg care behavior
was analyzed only for those days when at
least one egg sac was present in the colony.
Proportions were square-root arcsin trans-
formed and tested for normality (SAS Inc.,
1990).

The abdomen-size classes are ordinal num-
bers and can therefore be used in parametric
analysis only with caution. However, a re-
gression of body-fresh-weight on the abdo-
men-size class of 51 adult females showed
that the abdomen-size classes are very well
linearly correlated with body-fresh-weight
(see Results section). Therefore, I used ab-
domen-size estimates in analysis of covari-
ance (ANCOVA) as covariable. These AN-
COVA's tested for the dependence of web
maintenance behavior, attacking frequency,
proportion of time a spider stayed inside the
retreat and the proportion of time caring for
egg sacs on abdomen-size. To linearize the re-
lation between the dependent variable and the
covariable, I used the square-root of abdomen-
size in the ANCOVAs of web maintenance
and location, and the square of abdomen-size
in the ANCOVAs of attacking frequency and
egg caring. These four ANCOVA's included
further colony and individuals as factors, with
individual females nested within colonies and
repeated observations on females nested with
individuals. Colonies were tested over indi-
viduals. Type III sum of squares were calcu-
lated because the number of females was not
equal within the three colonies (Procedure
GLM, SAS, Inc, 1990).

RESULTS

Spider abdomen-size.—From 51 adult spiders a correlation between cephalothorax width, abdomen-size classification and body fresh weight was done. Cephalothorax width was poorly correlated with body fresh weight (Spearman rank correlation: $r_s = 0.288$, $P < 0.05$), and not correlated with abdomen-size class ($r_s = 0.017$, $P > 0.8$). The nine abdomen-size classes however, correlated nicely with body fresh weight ($r_s = 0.88$, $P < 0.0001$). A linear regression relating fresh weight to abdomen-size class gave the following equation: weight[mg] = 5.88 + 1.715 × size-class.

To test whether the abdomen-size classification is a suitable predictor of body fresh weight under field conditions, I calculated the change in abdomen-size class from each pair of abdomen-size class for each female observed on two successive observation days. The abdomen-size class of those spiders which were observed feeding for at least one hour increased significantly compared to those who had not fed for at least one hour (colony 1: difference of the mean size class change of feeding and no-feeding females = 0.47, $P < 0.0001$, $df = 240$; colony 2: diff. = 0.31, $P < 0.05$, $df = 174$; colony 3: diff. = 0.72, $P < 0.0001$, $df = 136$; t-tests; with the number of degrees of freedom corrected for repeated measures of some individuals: $P < 0.01$, $P = 0.06$, $P < 0.001$, respectively; comparisons were done excluding females within a period of three days before or after egg laying). I conclude that the abdomen-size classification method is appropriate to estimate spider fresh weight by viewing their abdomen-size while in colonies.

Mean abdomen-size did not differ among the three colonies (Fig. 1), although females differed within colonies. The mothers with the seven egg sacs (five sacs were newly found in colony 1 and one each in colonies 2 and 3) had the largest abdomens. Abdomen-size dropped drastically after the eggs were laid (Fig. 1). Fourteen females which disappeared for unknown reasons had significantly smaller abdomens than the egg-laying females after eggs had been laid ($t = 3.01$, $P < 0.05$). The egg-layers were also larger than 10 females which were found dead hanging in the web ($t = 7.8$, $P < 0.001$). These latter females had

Figure 1.—Mean abdomen sizes (± 1 SD) of adult females. Except for the three first estimates, data were pooled from the three colonies. Categories: total mean = mean abdomen size of all females; new adults = females which molted during the previous day into the adult instar; before and after egg laying = females on the day before and the day after they laid an egg sac, respectively; disappeared = last size estimate of females which disappeared for unknown reasons; starved = females which were found hanging dead in the web.

shown a gradual decrease in abdomen-size before their death, although their cephalothorax widths were within the range of adult females (mean 1.423, SD = 0.07). If their bodies were not removed from the web, they were taken by ants. It is not clear whether these females died because of old age or because they starved. Five females molted into the adult instar during the study. The mean abdomen-size of these "new adults" at the first day of adulthood was not different from the average female size (Fig. 1).

It is possible that spiders of the last juvenile instar were mistaken as adults, since the largest juveniles are nearly as large as small adults. However, I believe the chances for this mistake are very low. First, I observed no case in which an adult female disappeared and a new adult appeared at the same time, which would happen if a large juvenile (mistaken as adult) molted to become adult. Second, at the end of the study all marked females were taken to the laboratory and their cephalothorax widths measured. All widths were well in the range of widths determined earlier for adult females.

Abdomen-size and behavior.—Web maintenance behavior and prey-attacking frequency decreased with increasing abdomen-size,
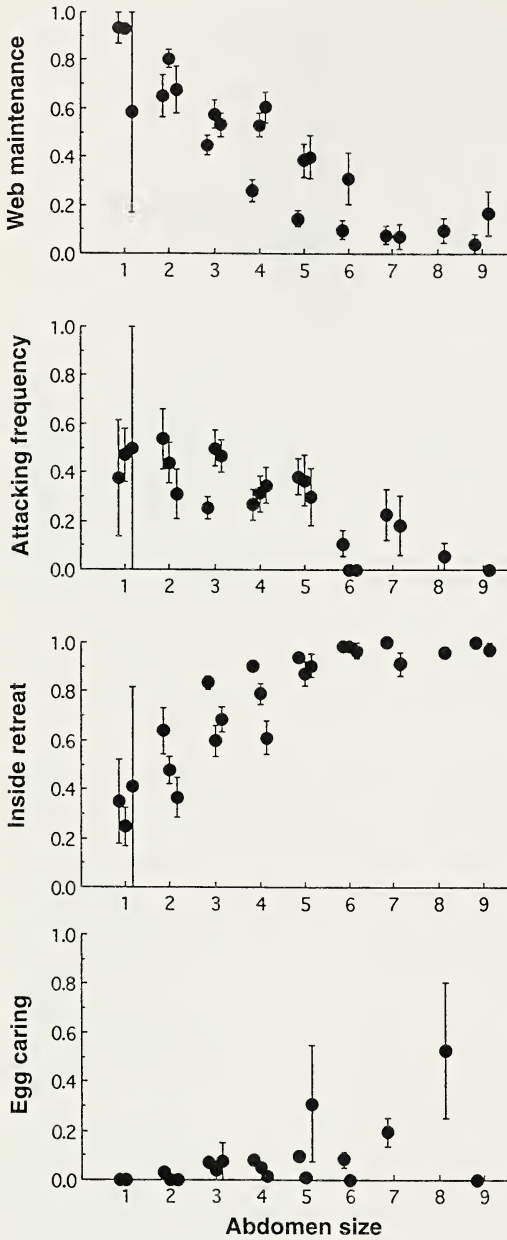
Figure 2.—Proportion of females (± 1 SE) showing four behavioral traits in relation to their abdomen size. Behavioral traits are the proportion of time a female does web maintenance, the proportion of females taking part in attacking prey, the proportion of time a female stayed inside the retreats and the proportion of time a female cares for eggs. Each point represents the mean of all females of each colony in the corresponding size class. To avoid overlap, means of colony 1 were shifted 0.15 size classes to the left and means of colony 3 were shifted 0.15 size classes to the right. Only points are included which represent the mean from at least two observations. Note that for some means the error bars fall within the dots.

while the tendency to stay inside the retreats and to care for egg sacs increased with increasing abdomen-size (Fig. 2, Table 1). No correlation was found for the relation between feeding time and abdomen-size (Spearman, $P > 0.3$). Further, Vollrath's (1986a) speculation that feeding time should be inversely related with attacking frequency was not confirmed here (correlation between mean feeding time and mean attacking frequency per female: $r = -0.04$, 0.21 and 0.18 for colonies 1, 2 and 3, respectively; $P > 0.5$). There was an inverse relation between mean feeding time and mean web maintenance frequency (Fig. 3; colony 1: $r_s = -0.66$, $n = 18$, $P < 0.005$; colony 2: $r_s = -0.46$, $n = 15$, $P < 0.1$; colony 3: $r_s = -0.66$, $n = 10$, $P < 0.05$).

Prey size and spider behavior.—The number of females attacking prey and the

Table 1.—Nested analysis of covariance (AN-COVA) for four behavioral traits (compare Fig. 2). Individual females were nested within colonies, repeated measures of individual females nested within females.

| Source	df	type-III SS	F	P
Web maintenance behavior ($r^2 = 0.53$)				
colony	2	2.5709	1.66	0.20
individuals	46	35.6073	4.57	0.0001
size	1	5.5916	32.99	0.0001
size*colony	2	1.4101	4.16	0.016
error	522	88.4777		
Attacking frequency ($r^2 = 0.24$):				
colony	2	4.6714	2.37	0.073
individuals	46	38.8703	2.23	0.0001
size	1	2.0035	5.28	0.022
size*colony	2	3.9087	5.15	0.006
error	419	158.901		
Location of spider (inside retreat) ($r^2 = 0.50$):				
colony	2	4.0969	2.69	0.078
individuals	45	34.2601	5.32	0.0001
size	1	8.1441	56.94	0.0001
size*colony	2	3.3211	11.61	0.0001
error	570	81.5221		
Egg care frequency ($r^2 = 0.26$):				
colony	2	1.0652	4.64	0.015
individuals	40	4.5868	2.08	0.0002
size	1	0.2282	4.14	0.04
size*colony	2	0.4887	4.44	0.012
error	419	23.0815		
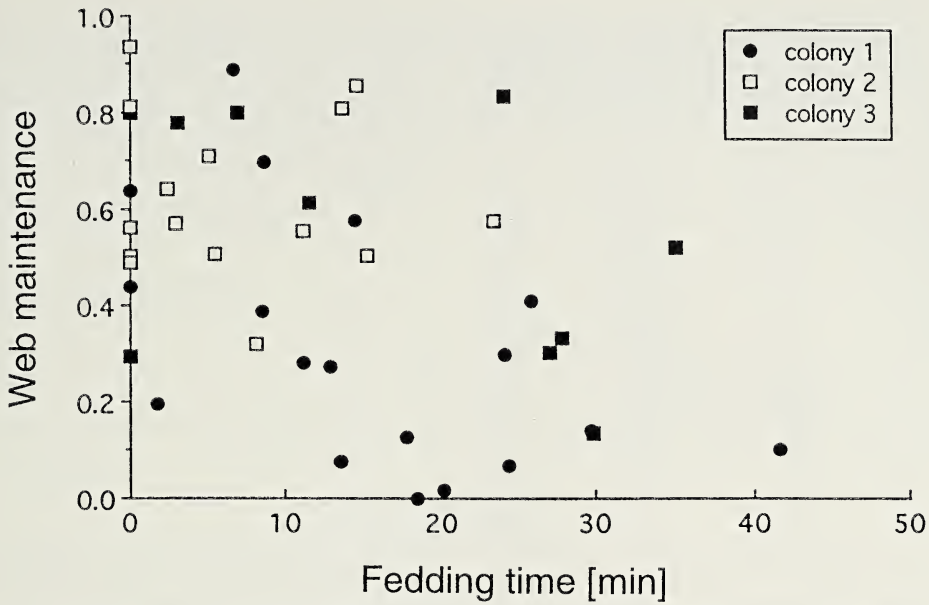
Figure 3.—The relation of mean female feeding time and web maintenance frequency. Each point represents the mean of one adult female, which was observed for at least five days. Feeding time represents the mean time a female spend feeding on one prey item. Pearson correlation coefficient for the pooled data: $r = -0.47$ ($P < 0.002$, $n = 43$).

number of females feeding on the captured prey increased with prey size (Table 2). The same is true for the number of females feeding without prior participation in attacking. Such opportunistic feeders are under represented when prey size is small, but are common for larger prey items (Fig. 4). Visualization of all four regressions in Table 2 suggests approximate linear relationships, although given the small sample size and the relatively low r^2 values non-linearity would be very difficult to detect.

About 50% of feeders on small prey (< 8 mm) had been outside the retreats at the moment the prey came into the snare (Fig. 5). For larger prey, almost all the spiders which took part in feeding were inside the retreats

when the prey came in (Fig. 5). The exceptional increase for the largest prey class in Fig. 5 is explained by the fact that in two cases the prey was so large that all adult females were able to take part in feeding. In summary, when food items are small, they were in many cases caught and eaten by females which waited outside the retreats. In contrast, larger prey were caught by all spiders (regardless of whether they were inside or outside the retreat when the prey came in), but were mainly eaten by those spiders which came from inside the retreat to join the attack.

Since spiders outside of retreats took part in most attacks, their under-representation among feeders on large prey requires an explanation. In 8 of 9 observed cases of direct

Table 2.—Regression of various measures of participation in prey handling on the size of prey (mm). Feeding time is the time from start of feeding on the prey until the last female left the prey. Data from all three colonies were pooled. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

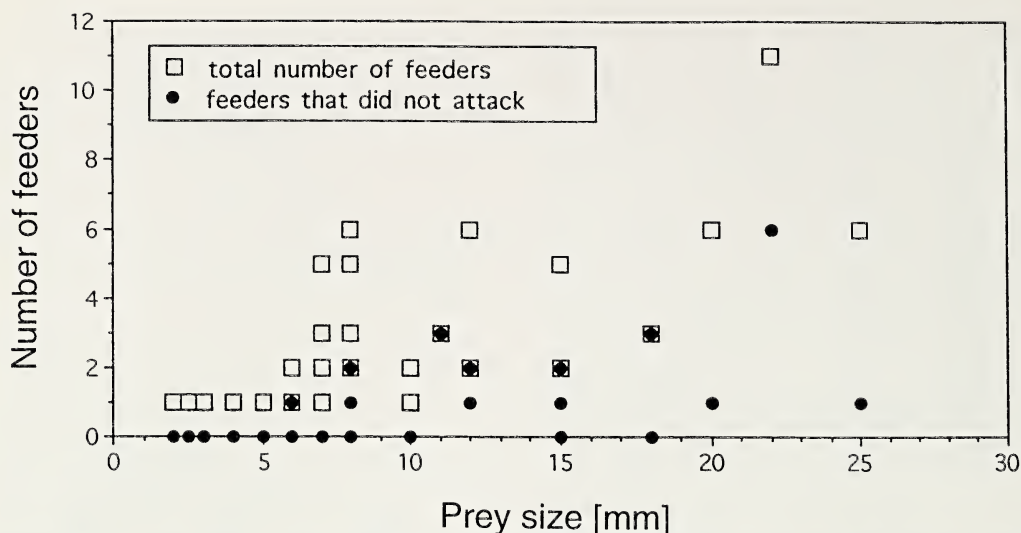| Trait	Intercept	Slope	r^2	n
Feeding time [min]	−0.438	0.374	0.58***	43
Total number females attacking prey	1.966	0.223	0.23**	44
Total number feeders on prey	0.698	0.227	0.38***	48
Number of feeders which did not attack prey	−0.502	0.128	0.33***	42

Figure 4.—Total number of feeders and number of feeders which did not take part in attacking prey (opportunistic feeders), in relation to prey size. Points are only included when the number of feeders were precisely known. Note that for small prey items (< 6 mm) no opportunistic feeders were observed.

interaction between two adult females over prey, abdomen-size class taken before the interaction was observed differed. In 7 of these 8 cases the larger female won the feeding position on the prey (paired t-test for size difference: diff. = 1.33, SE = 0.44, $P < 0.05$).

Mortality.—During this study I observed nine females killed by predators (1 giant damselfly, 1 mantid, 1 wasp, 4 jumping spiders, 2 orb-web spiders), whilst outside the retreats in the more peripheral parts of the colonies. All 9 were outside the retreat when captured; 6

died during web maintenance, 3 while waiting in the snare for prey.

Food restriction experiment.—The role of hunger in creating an asymmetric distribution of behavior was tested by the re-introduction of well-fed and starved females into their original colonies. The starved females spent on average 65% more time outside the retreats than the well-fed females and participated 33% more in web maintenance (Table 3). Starved females tended to attack more, regardless of whether they were inside or outside the retreats at the moment the prey came in (Table 3). This was found even if only those spiders that were inside the retreats when the prey came in were included in the analysis (Table 3). Not enough data were collected in this experiment to make a meaningful analysis with respect to feeding time.

DISCUSSION

Behavioral asymmetry and body size structure.—Short-term observation of individually marked adult females showed that behavioral asymmetry exists in the colonial spider *Anelosimus eximius*. This asymmetry seems to be governed by differences in body weight and hunger status. As already recorded by Vollrath & Rohde-Arndt (1983) only females of high body weight reproduce. In contrast, females with small abdomens conduct
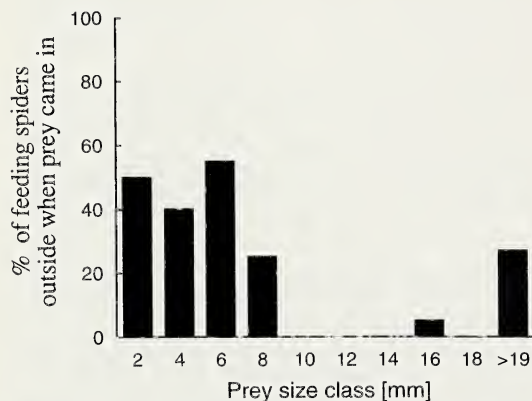

Figure 5.—Percentage of females taking part in feeding, which were outside the retreat at the moment prey of a given size class came in. Total sample size is 131.

Table 3.—Comparison between well-fed and starved females. Behavioral means represent the mean proportion of each of the three females for each of three days. Likelihood ratio tests (SAS Inc. 1990) were used to test frequencies of the given behavior against the alternative behavior (inside versus outside retreat, participation *versus* non-participation). $df = 1$ in all cases. A combined probability tests (Sokal & Rohlf 1981) combining the three colonies was significant for all 4 traits ($P < 0.01$).

Behavior	Colony	Fed	Starved	χ^2	P
Time outside retreat	4	0.068	0.955	171.6	0.0001
	5	0.189	0.973	137.9	0.0001
	6	0.676	0.973	25.9	0.0001
Participation in web maintenance	4	0.625	0.937	35.1	0.0001
	5	0.427	0.865	45.0	0.0001
	6	0.611	0.854	22.3	0.0001
Attacking	4	0.167	0.500	2.84	0.09
	5	0.091	0.615	7.73	0.005
	6	0.111	0.667	12.64	0.0001
Inside and attack	4	0.182	0.500	1.42	0.23
	5	0.111	0.500	3.23	0.07
	6	0.063	0.625	8.93	0.003

most of the web maintenance and usually stay outside the retreats. They take part in most prey-attacks, but feeding is limited to small prey items. Females of intermediate weight (i.e., abdomen-size classes 4–5) spend most of their time in the retreats, contribute little to web maintenance but take part in attack and feeding of larger prey items. By these means they may gain enough resources to become large and to reproduce. The largest females rarely take part in attacking or web maintenance, rarely leave the retreats, but do most of the egg sac care. These large, competitive females gain access to food by joining feeding companies or chasing smaller spiders away, as proposed by Vollrath & Rohde-Arndt (1983), Vollrath (1986a) and Rypstra (1993).

The altered behavior of large (size classes 5–9) females is not very surprising, given a high likelihood that they will lay eggs soon. Therefore this does not support the existence of a behavioral asymmetry. However, Fig. 2 shows that size related behavioral asymmetry is found even if only smaller size classes are considered. For example, the proportion of females inside the retreats was about 30% for females of abdomen-size class 1 and about 70% for those of size class 4. Likewise, web maintenance behavior decreased from 75 to 50% from size classes 1 to 4.

The strong tendency for small, possibly less competitive, spiders to stay outside the retreats may be explained as an optimal foraging strategy to gain access to at least some small food items, since females feeding on small prey were rarely joined by other females which did not take part in attacking (Fig. 4). Monopolization of small prey was also observed by Pasquet & Krafft (1992) for *Anelosimus eximius* and by Brach (1977) for *A. studiosus* (Hentz 1850). Minute insects are sucked out on the spot by one or two spiders. The observation that small prey were ignored by *A. eximius* in laboratory colonies (Brach 1975) may be explained by the better nutritional status of laboratory spiders and a correspondingly higher threshold to response to web vibration (Vollrath 1986a). Small prey, e.g., small dipterans, generate less vibration than larger prey and may only be detected by spiders nearby, i.e., outside the retreat. This idea is supported by my observation that sometimes small insects caught in the peripheral part of the web were not recognized by any of the females in the colony (D.E., pers. obs.). Alternatively, the low dry weight of small prey (Pasquet & Krafft 1992) might only be profitable for smaller spiders and are therefore ignored by larger colony mates.

The strong tendency of small spiders to stay outside the retreats may, however, be explained as altruistic behavior, evolved to maximize the success of the highly inbred colonies rather than the individual (Vollrath 1986a; Rypstra 1993). Individual selection on plasticity in foraging behavior in spiders with different nutritional status might have pre-dated the evolution of sociality in spiders, suggest-

ing that the advantages of such plasticity for the colony could have played a role in the evolution of sociality as found in *A. eximius*.

Size-dependent behavioral asymmetry as described here has not been recorded in earlier studies. Vollrath & Rohde-Arndt (1983) reduced the body weight variance at the start of their study, which reduced the likelihood of detecting differences associated with body weight. The smallest females in my study were clearly of lower weight than females in the single colony of Vollrath & Rohde-Arndt (1983). The frequent occurrence of low body weights and general decline in my colonies might be a result of the poor feeding conditions during the dry season in Central Panama (Lubin 1978; Vollrath 1986b).

In summary, behavioral asymmetry with respect to prey-attack, web maintenance and reproduction is demonstrated by this study on three colonies of *A. eximius*. The data agree with earlier observations on the same species. The important question to ask now is whether a consistent size asymmetry is maintained over longer time periods.

Stability of size structure over time and food levels.—This study does not allow us to distinguish between a permanent size-structured behavioral asymmetry or a temporal (i.e., age related, Lubin (1995)) asymmetry. My study provides only a one month snapshot in time, which is shorter than the adult life span of *A. eximius* females. In the following I suggest four arguments in favor of a stable size (i.e., independent of the adult age of a female) hierarchy; however, it should be noted that only a much longer study will be convincing on this point.

First, the manipulation experiment with well-fed and starved females suggests however that age is of less importance. The experiment indicates that nutritional status explains a great deal of the observed behavioral asymmetry, although the remaining variance might well be age related.

Second, a positive correlation of spider size with feeding time could strengthen an existing size structure. Although my data do not support such a correlation, I believe that the true relationship between spider size and feeding success was underestimated. In contrast to small prey items, feeding time on large prey items was strongly underestimated because feeding often exceeded the observation period

and extended late into the night (D.E. pers. obs.; Rypstra & Tirey (1991)). Thus feeders joining the prey after the end of my observation periods escaped my attention. Reproducing spiders stop feeding a few days before they lay eggs (A.L. Rypstra pers. comm.), which reduces feeding time estimates of large spiders. Feeding time poorly estimates food uptake which varies in relation to prey size and the number of cofeeders, as shown for other colonial spiders (Ward & Enders 1985; Riechert et al. 1986).

Third, the relationship between spider size, behavior and prey size suggests that the stability of the female size hierarchy depends on the frequency and size of the incoming prey. In Panama, Peru and French Guiana it was found that in *A. eximius* colonies most prey was about 10–15 mm, which is 2–3× longer than adult *A. eximius* (Nentwig 1985; Rypstra 1990; Rypstra & Tirey 1991; Pasquet & Krafft 1992). Furthermore, 76% of incoming prey-dry-weight comes from prey items longer than 20 mm (Pasquet & Krafft 1992), suggesting that absolute feeding success of small females waiting outside the retreats for small prey is low so that changes in their relative position in the size hierarchy are less likely. Larger females get much more food by feeding on the larger and more common prey.

Fourth, from what was said before it appears that after periods of high prey capture success, even the smallest females might gain sufficient resources to become reproductive and thus overturn the reproductive asymmetry (Elgar & Godfray 1987). However, Rypstra (1993) showed in laboratory experiments that this seems to be the case only when prey is small. Strong asymmetry was observed when the spiders were fed exclusively on large prey. This indicates that food quality (size) but not quantity (number of flies) determines behavioral asymmetry in *A. eximius* (Rypstra 1993). An interesting point here is the observation that the size range of captured prey tends to increases with increasing colony size (Ward 1986; Pasquet & Krafft 1992). Thus, feeding asymmetry and the resulting reproductive asymmetry could be expected to become more pronounced as colonies grow.

In summary, stability of the size hierarchy in *A. eximius* colonies is likely to depend on the size structure of its natural prey. This problem can only be settled with more data

on the plasticity of lifetime reproductive success of individual spiders across the natural range of prey.

Mortality.—In colonies with high degrees of relatedness among colony members, strategies which maximize the survival of females at times when their reproductive value is high would be advantageous for the whole colony even if it reduced survival of non- or post-reproductive spiders (Wilson 1971; Jarvis 1981). All nine females which were seen to be captured by predators were located outside the retreats. It is not clear whether the web maintenance activity attracts predators, but a higher mortality risk on the periphery of a colony is reported from another colonial spider (Rayor & Uetz 1990). A higher mortality rate in females not involved currently in reproduction is indirectly supported by the finding that the 14 adult females which disappeared from the colonies were smaller on average than reproductive spiders. I suspect that these spiders became victims of predators rather than emigrated, because 1) I never found any marked spiders outside the colonies, 2) twice I found a single spider leg hanging in the snare after a spider disappeared, and 3) Vollrath (1982) reported that only females with swollen abdomens (presumably gravid females) emigrate, but the spiders which disappeared from my colonies were of small abdomen size (Fig. 1). In the light of this asymmetric mortality, future studies should include mortality in relation to attacking frequency (Vollrath & Rohde-Arndt 1983) and defense against intruders (Vollrath & Windsor 1986).

CONCLUSION

The social structure in colonies of *Anelosimus eximius* appears to be governed by behavioral asymmetry. This study shows that large competitive females reproduce, take care of egg sacs and avoid leaving the safe retreats. Small females do most of the foraging in terms of web maintenance, and have a higher risk of mortality by predators. The proximate cause of the asymmetry seems to be differences in nutritional condition and foraging behavior among females, as was shown in manipulation experiments with starved and well-fed spiders. Age effects could not be ruled out; however; the manipulation experiment showed that independent from the age of a female her nutritional status plays an im-

portant role. The ultimate cause might be that colonies with higher reproductive asymmetry produce more egg sacs then those with little or no asymmetry, suggesting that the maintenance of the size structure is beneficial for the whole colony (Rypstra 1993). More detailed studies on the food flow within colonies and observations over longer time periods are needed to predict who will be able to reproduce and whether the behavioral asymmetry is stable of time.

ACKNOWLEDGMENTS

LITERATURE CITED

Anderson, J.F. 1974. Response to starvation in the spiders *Lycosa lenta* Hentz and *Filistata hibernalis* (Hentz). Ecology, 55:576–586.

Avilés, L. 1986. Sex-ration bias and possible group selection in the social spider *Anelosimus eximius*. American Nat., 128:1–12.

Brach, V. 1975. The biology of the social spider *Anelosimus eximius* (Araneae: Theridiidae). Bull. Southern California Acad. Sci., 74:37–41.

Brach, V. 1977. *Anelosimus studiosus* (Araneae: Theridiidae) and the evolution of quasisociality in theridiid spiders. Evolution, 31:154–161.

Buskirk, R.E. 1981. Sociality in Arachnida. Pp. 281–367, *In* Social Insects. (H.R. Hermann, ed.). Academic Press, New York.

Christenson, T.E. 1984. Behaviour of colonial and solitary spiders of the theridiid species *Anelosimus eximius*. Anim. Behav., 32:725–734.

Elgar, M.A. & H.C.J. Godfray. 1987. Sociality and sex ratios in spiders. Trends Ecol. Evol., 2:6–7.

Foelix, R.F. 1985. Biology of spiders. Harvard Univ. Press, Cambridge.

Jarvis, J.U.M. 1981. Eusociality in a mammal: cooperative breeding in naked mole-rat colonies. Science, 212:571–573.

Levi, H.W. 1956. The spider genera *Neottiura* and *Anelosimus* in America (Araneae: Theridiidae). Trans. American Micros. Soc., 75:407–422.

Levi, H.W. 1963. The American spiders of the genus *Anelosimus* (Araneae: Theridiidae). Trans. American Micros. Soc., 82:30–48.

Lubin, Y.D. 1978. Seasonal abundance and diver-

sity of web-building spiders in relation to habitat structure on Barro Colorado Island, Panama. J. Arachnol., 6:31–51.

Lubin, Y.D. 1995. Is there division-of-labour in the social spider *Achaeranea wau* (Theridiidae)? Anim. Behav., 49:1315–1323.

Nentwig, W. 1985. Social spiders catch larger prey: a study of *Anelosimus eximius* (Araneae: Theridiidae). Behav. Ecol. Sociobiol., 17:79–85.

Pasquet, A. & B. Krafft. 1992. Cooperation and prey capture efficiency in a social spider, *Anelosimus eximius* (Araneae, Theridiidae). Ethology, 90:121–133.

Rayor, L.S. & G.W. Uetz. 1990. Trade-offs in foraging success and predation risk with spatial position in colonial spiders. Behav. Ecol. Sociobiol., 27:77–85.

Riechert, S.E., R. Roeloffs & A.C. Echternacht. 1986. The ecology of the cooperative spider *Agelena consociata* in equatorial Africa (Araneae: Agelenidae). J. Arachnol., 14:175–191.

Roeloffs, R. & S.E. Riechert. 1988. Dispersal and population structure of the cooperative spider *Agelena consociata* in west African rain forest. Evolution, 42:173–183.

Rypstra, A.L. 1990. Prey capture and feeding efficiency of social and solitary spiders: a comparison. Acta. Zool. Fennica, 190:339–343.

Rypstra, A.L. 1993. Prey size, social competition and the development of reproductive division of labor in social spider groups. American Nat., 142:868–800.

Rypstra, A.L. & R.S. Tirey. 1991. Prey size, prey perishability and group foraging in a social spider. Oecologia (Berlin), 86:25–30.

SAS Institute, Inc. 1990. SAS/STAT, Version 6.06, Cary, North Carolina: SAS Institute, Inc.

Smith, D.R.R. 1986. Population genetics of *Anelosimus eximius* (Araneae, Theridiidae). J. Arachnol., 14:201–219.

Vollrath, F. 1982. Colony foundation in a social spider. Z. Tierpsychol., 60:313–324.

Vollrath, F. 1986a. Eusociality and extraordinary sex ratios in the spider *Anelosimus eximius* (Araneae: Theridiidae). Behav. Ecol. Sociobiol., 18:283–287.

Vollrath, F. 1986b. Environment, reproduction and the sex ratio of the social spider *Anelosimus eximius* (Araneae: Theridiidae). J. Arachnol., 14:267–281.

Vollrath, F. & D. Rohde-Arndt. 1983. Prey capture and feeding in the social spider *Anelosimus eximius*. Z. Tierpsychol., 61:334–340.

Vollrath, F. & D. Windsor. 1986. Subsocial and social *Anelosimus*: a comparison especially of nest defense. Pp. 295–298, *In* Proc. 9th Internatl. Arachnol. Congress. (W.D. Eberhard, Y.D. Lubin, & B.C. Robinson, eds.). Smithsonian Institution Press, Washington.

Ward, P.I. 1986. Prey availability increases less quickly than nest size in the social spider *Stegodyphus mimosarum*. Behaviour, 97:213–225.

Ward, P.I. & M.M. Enders. 1985. Conflict and cooperation in the group feeding of the social spider *Stegodyphus mimosarum*. Behaviour, 94:167–182.

Wilson, E.O. 1971. The Insect Societies. Harvard Univ. Press, Cambridge.

Wolda, H. 1978. Seasonal fluctuations in rainfall, food and abundance of tropical insects. J. Anim. Ecol., 47:369–381.

CHEMICAL AND BEHAVIORAL DEFENSES OF A NEOTROPICAL CAVERNICOLOUS HARVESTMAN: *GONIOSOMA SPELAEUM* (OPILIONES, LANIATORES, GONYLEPTIDAE)

Pedro Gnaspini: Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Caixa Postal 11461, 05422-970, São Paulo, SP, Brazil

Alberto José Cavalheiro: Departamento de Química Fundamental, Instituto de Química, Universidade de São Paulo, 05508-900, São Paulo, SP, Brazil

ABSTRACT. *Goniosoma spelaeum* (Mello-Leitão 1932), a cavernicolous species in the Ribeira Valley, southeastern Brazil, was studied in the field and laboratory. The defensive behaviors were: nipping with the chelicerae; delivery of a sharp pinch with the fourth coxae and femora; rapidly running away; dropping from the cave ceiling and remaining concealed against the substrate; and emission of a chemical defense compound. The delivery mechanisms of the defensive secretion were either by spreading the substance on its own body through a lateral groove, or by projecting it as a jet directly at the aggressor. The defensive substance is a mixture of enteric fluid, which runs from the mouth into ventral and lateral channels, with quinones collected from the scent gland openings located next to the lateral margins of coxae II. Electron microscope analysis of the external structure of the exocrine gland opening revealed a second aperture which could be responsible for the jet emission. Two quinones (2-ethyl-1,4-benzoquinone and 2,3,5-trimethyl-1,4-benzoquinone) were identified from the defensive secretion; the first is reported herein for the first time in opilionids. Four other species of *Goniosoma* Perty 1833 from epigean and hypogean environments showed similar behaviors.

Studies on the defensive behavior of harvestmen are relatively few, and most deal with species of suborder Palpatores from the Northern Hemisphere. In this group, autotomy of legs is suggested as the most important defensive behavior (Berland 1949; Edgar 1971; Kaestner 1968). Also common in Palpatores is the shaking of the body (Berland 1949) and the presence of bright white bands on the distal portions of two or more legs (J. Cokendolpher pers. comm.), which probably hinders the identification and exact location of the harvestman's body.

Some harvestmen feign death and become rigid (Cokendolpher 1987; Eisner et al. 1971). Long-legged species run away rapidly (Bristowe 1925; Edgar 1971). Others drop to the ground, where they stay motionless and concealed amongst the substrate, thus confounding their predators (Duffield et al. 1981; Edgar 1971; Hillyard & Sankey 1989). Some Gonyleptidae (suborder Laniatores), when taken in hand, flex their fourth legs quickly toward the body in order to deliver a sharp pinch to the aggressor between the armature of both the coxae and femora. This has been reported for *Goniosoma longipes* (Roewer 1913) and *G. roridum* Perty 1833 from Ouro Preto, Brazil (Bristowe 1925) and *Acanthopachylus aculeatus* (Kirby 1819) from Uruguay (Capocasale & Bruno-Trezza 1964).

However, the best known defensive behavior, which is considered most effective in Laniatores and Cyphophthalmi, is chemical exudation (see review in Eisner et al. 1978). The animals secrete chemical substances from a pair of exocrine glands ("scent glands") which open on the cephalothorax next to the lateral margins of coxae I in Palpatores, or coxae II in Laniatores and between coxae II and III in Cyphophthalmi (Juberthie 1961, 1976). The mechanisms of delivery of the defensive secretion in harvestmen are diverse, as summarized by Acosta et al. (1993).

Chemical analyses of defensive exudates have shown that, among the Laniatores, the

Gonyleptoidea produce a variety of alkylated benzoquinones and phenols (Eisner et al. 1971, 1977; Estable et al. 1955; Fieser & Ardao 1956; Roach et al. 1980), and the Travunioidea produce mainly terpenoids (Ekpa et al. 1984). In contrast, among the Palpatores, the Leiobuninae secrete short-chain acyclic ketones and alcohols (Blum & Edgar 1971; Ekpa et al. 1985; Jones et al. 1976, 1977; Meinwald et al. 1971), whereas the Phalangiinae produce naphthoquinones, which were considered to be rare as natural products (Wiemer et al. 1978). No chemical data are available for species of Cyphophthalmi, but the orangish coloration of the gland contents in at least one *Siro* species may suggest the presence of a quinone (J. Cokendolpher pers. comm.).

Studies on the chemistry of exocrine secretions of harvestmen have been restricted to species from the Northern Hemisphere, with two exceptions: *Acanthopachylus aculeatus* from Uruguay (Estable et al. 1955; Fieser & Ardao 1956) and *Pachyloidellus goliath* Acosta 1993 from Argentina (Acosta et al. 1993). Furthermore, all species studied dwell in epigean environments.

This paper is part of a general natural history study of cavernicolous harvestmen, conducted from November 1991 to August 1993 in the Ribeira Valley, southeastern Brazil (see Gnaspini 1995, 1996). In the present study, we report on the defense of *Goniosoma spelaeum* (Mello-Leitão 1932) (Laniatores, Gonyleptidae, Goniosomatinae), a cavernicolous species in the Ribeira Valley, São Paulo state, southeastern Brazil. Observations on other *Goniosoma* species (*G. proximum* (Mello-Leitão 1922), *G. varium* Perty 1833 and two undescribed species near *G. badium* C.L. Koch 1839) were made occasionally.

METHODS

The harvestmen studied were either observed in the field or in an underground laboratory in São Paulo, with environmental conditions similar to those of the caves in which they were captured. Behavioral analysis was conducted both while handling the specimens and later, based on video tapes taken during handling.

Goniosoma spelaeum is a large harvestman—the adults have a body about 1 cm long and 1 cm wide, and often reach more than 20 cm in diameter with the legs spread. They are very common and widely distributed in caves throughout the Ribeira Valley, in São Paulo state (see Gnaspini 1995, 1996).

During the field study, more than 2000 individuals of *G. spelaeum* (adults and juveniles) were captured, handled and marked (in order to allow individual recognition for another study). Defensive behavior was elicited and observed on most of those specimens. Observations on *G. proximum*, *G. varium* and two undescribed species (related to *G. badium*) were made occasionally. Besides handling the animals, defensive behavior could also be induced by shining a light on them or by approaching them. Emission of chemical secretion of *G. spelaeum* was also observed under a stereomicroscope in the laboratory.

Defensive secretions were collected in the laboratory directly from 10 live specimens of *G. spelaeum* after its release. This secretion was diluted by the animals with oral fluids, as is common in other harvestmen studied (e.g., Eisner et al. 1971). To obtain concentrated samples, five freshly killed specimens were dissected and the glandular contents were aspirated into glass tubes. Chemical analyses were made with a Varian 2400 gas chromatograph using a capillary column DB-5 coupled with a Finningan MAT ITDS80 mass spectrometer. The substances were identified by comparing their mass spectra with those published by McLafferty & Stauffer (1989). The external morphology of the gland opening was studied under a Zeiss DSM 940 scanning electron microscope.

A series of *G. spelaeum* vouchers was deposited in the Museu de Zoologia da Universidade de São Paulo (MZSP).

RESULTS

The defensive behaviors observed in *Goniosoma spelaeum* included nipping with the chelicerae, delivery of a sharp pinch with the fourth coxae and femora, rapid running away, dropping from the cave ceiling, and emission of a chemical defense compound. The defensive substance is a mixture of enteric fluid, which runs from the mouth into ventral and lateral channels, with quinones collected from the gland opening located next to coxa II. The delivery mechanisms of the defensive secretion were either by spreading the substance on its own body through a lateral groove, or by projecting it as a jet directly at the aggressor.
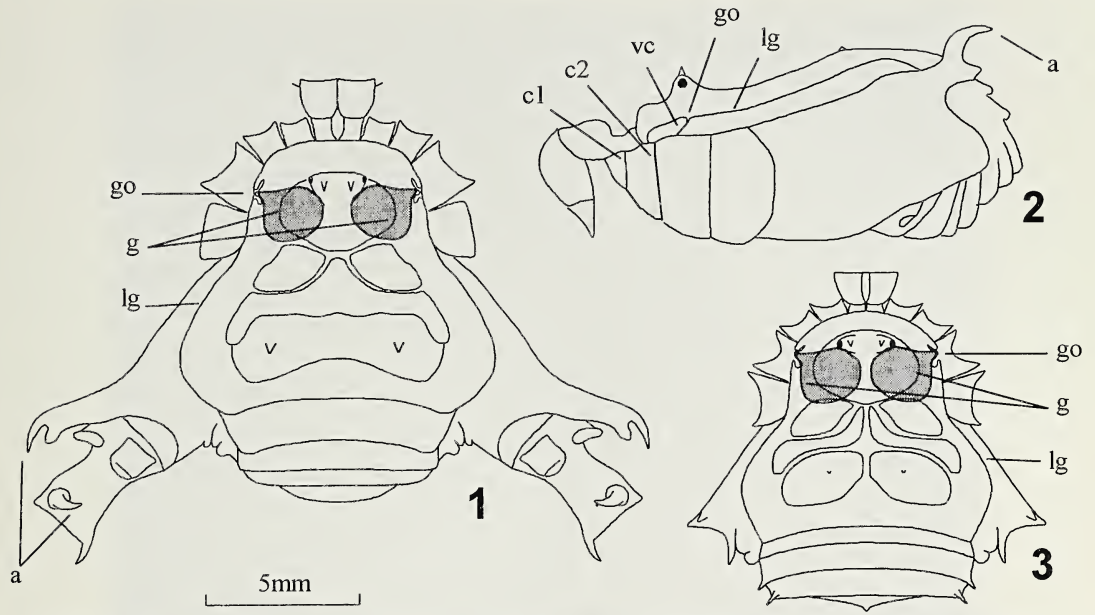
Figures 1–3.—*Goniosoma spelaeum*, habitus of adult male and female, showing defense features. 1, Dorsal view, male; 2, Lateral view, male; 3, Dorsal view, female. *a* = armature of coxa and trochanter; *c1* = channel between coxae of pedipalp and leg I; *c2* = channel between coxae of legs I and II; *g* = glands (hatching); *go* = gland opening; *lg* = lateral groove; *vc* = vertical channel connecting *c1* and *c2* with *lg*.

Gland opening and fluid displacement.— All *Goniosoma spelaeum* harvestmen have one pair of internal glands which open dorso-laterally over coxae II (Figs. 1–3). The discharge of these glands generally mixes with enteric fluid, as will be discussed in the next section. The enteric fluid, coming from the mouth, reaches the gland openings by capillarity through a sequence of channels (as in Figs. 1–3). First, there are two pairs of ventral channels—one is located between the coxae of the pedipalps and legs I (*c1* of Fig. 2); the other lies between the coxae of legs I and II (*c2*), and its white color sharply contrasts with the yellowish coxae. Observations with a stereomicroscope revealed that flow through channel *c2* seems to be more common than through *c1*; however, the position in which the specimen is placed for examination may influence the direction the fluid travels. Independently, these ventral channels reach a horizontal lateral channel defined within the soft pleura between the dorsal scutum and the coxae insertions. Finally, just in front of the gland opening, there is a vertical channel (*vc*, which is actually somewhat oblique), which connects the lateral channel with the lateral groove (*lg*).

In some cases the fluid may run by capillarity through the lateral groove, collecting posteriorly on coxae IV, as will be discussed later.

Whereas there is a single gland opening in other opilionids (e.g., Juberthie 1961, 1976), in *G. spelaeum* the structure of the gland opening region is more complex (Fig. 4). In addition to the actual gland opening located at the lateral margin of the scutum (*go* of Fig. 4), there are two secondary outlets located dorso-laterally and connected to "*go*" by very short channels: one anterior (a notch, *ga*), and one posterior (*gp*, with its internal integument covered with several small sharp projections, as in Fig. 5). Probably, after being released by the actual opening (*go*), the secretion runs anteriorly to *ga* or posteriorly to *gp*. Unfortunately, release through these openings was not observed through a microscope, and this hypothesis is based on the morphology of the region and on observations of the path taken by the fluid running nearby, and deserves further investigation. Actually, the running fluid baths the posterior opening when coming from the lateral channel towards the lateral groove. Observations made with a microscope

Figure 4.—*Goniosoma spelaeum*, dorsal view of left lateral margin, showing region of gland opening. *ac, ac⁺* = dorsal apophyses of coxa II; *dt* = tubercle dorsal to the gland opening; *ga* = anterior gland outlet (notch); *go* = gland opening; *gp* = posterior gland outlet; *lg* = lateral groove; *sp* = sensitive peg; *vc* = vertical channel which connects channels between coxae coming from the mouth with the lateral groove just in front the gland opening. Scale = 200 μm.

did not clearly reveal if this bath occurs over or through the posterior opening.

Besides a large dorsal apophysis on coxae I and II, as on *Pachyloidellus goliath* (Acosta et al. 1993), *G. spelaeum* has three small dorso-lateral apophyses on coxae II directed towards the gland opening (*ac*, Fig. 4). The larger anterior apophysis (*ac⁺*) is placed exactly over the position where the ventral channel *c2* meets the lateral channel.

The lateral groove, into which the defensive substance is released by the gland opening, is smooth and very shallow in *G. spelaeum* and has several pegs (probably sensory, as their shape is similar to sensorial pegs of other arthropods) along its margin (Fig. 4). The exact function of these pegs has not been studied. The defensive fluid baths these pegs as it runs

along the groove. The lateral groove starts slightly anterior to the gland opening and defines a continuous passage for the fluid coming from the ventral channels via the vertical channel and the lateral groove (Fig. 4). Thus, the secretion from the gland is released directly into the running enteric fluid from the mouth.

Chemical defensive behavior.—In the following discussion we use the codes for the mechanisms of delivery as proposed and listed by Acosta et al. (1993). Besides creating a "chemical shield" around their bodies, harvestmen may squirt the exudate as a jet or administer it by dabbing with the legs onto an aggressor. All species of *Goniosoma* considered in this study showed two of these behaviors: chemical shield and squirting. However,
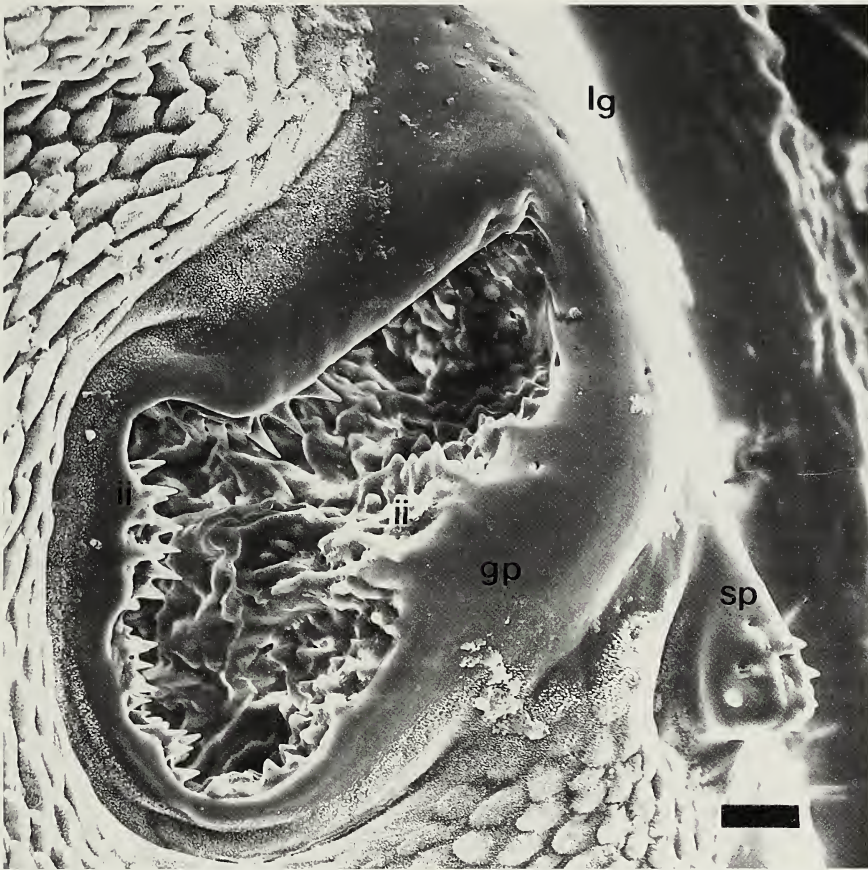
Figure 5.—*Goniosoma spelaeum*, dorsal view of right lateral margin. Detail of the posterior gland outlet, showing internal integument which is covered with sharp projections. *gp* = posterior gland outlet; *ii* = internal integument; *lg* = lateral groove; *sp* = sensorial peg. Scale = 20 μm.

we did not find a preference for one or the other delivery mechanism—the same specimen would either emit a jet or form a shield during subsequent handling. Leg dabbing was not observed.

In the *G. spelaeum* mechanism of "displacement of the liquid along the lateral area of the scutum" (coded as 2.2. by Acosta et al. 1993), the enteric fluid passes in front of the opening, where it may collect some secretion, and runs through the lateral groove down to coxae IV, where it forms a droplet (as in Figs. 6, 7). It should be noted that the mixing may not occur. Sometimes, the coxal droplet contains only enteric fluid, as indicated by its lack of smell and clear color, as in Fig. 6. This droplet may stay clear, i.e., the animal may not release secretion into it. This probably occurs when there is no secretion left in the gland or when the animal does not consider

releasing it. Secondly, the secretion can be released after the droplet is formed. In this case, the clear droplet (as in Fig. 6) becomes turbid and yellowish (as in Fig. 7). Thirdly, the secretion can be released while the enteric fluid is running in front of the gland opening. In this case, the droplet which is formed, as well as the fluid over the lateral groove, is already turbid and yellowish (also as in Fig. 7). Therefore, the same final aspect (turbid droplet) may take one or two steps to be achieved. Then, this droplet is retained on the coxae IV, where it evaporates. The formation of droplets, always on coxae IV, is not a normal condition of the species, occurring only after handling, and it is thus probably a defensive behavior.

Another common defensive behavior of *G. spelaeum* was the "emission in form of a fine jet upwards and backwards" (coded as 3.1. by
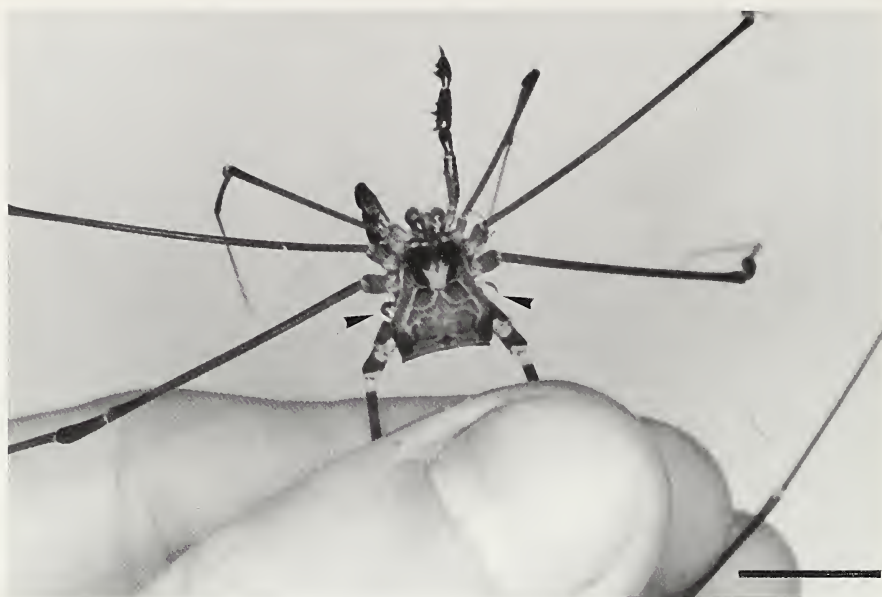
Figure 6.—*Goniosoma spelaeum*, dorsal view, showing two droplets (arrows) formed only by enteric fluid, which is clear. Scale = 10 mm.

Acosta et al. 1993). In *G. spelaeum*, the jet is emitted directly from the gland opening and extends at least 5 cm, and very often 10 cm or more. It can be emitted in any direction, even forward. Whichever was the region of the animal body handled, the jet emitted usually reached the observer's hands. This jet is bright yellow and becomes reddish after a few seconds. When seized by the fourth pair of legs, *G. spelaeum* may also turn its body quickly backwards while emitting the jet, probably enhancing the chance of the substance hitting and spreading upon the aggressor.

Figure 7.—*Goniosoma spelaeum*, lateral view, showing the turbid droplet of secretion (arrow) formed by the mixture of enteric fluid and defensive exudate. Scale = 10 mm.

Chemical analysis of the defensive exudate.—The odor and yellowish color of the defensive exudate of *Goniosoma spelaeum*, combined with the fact that it stained human skin with a reddish spot, suggested that it might contain one or more quinones. Laboratory analyses confirmed the mixture of benzoquinones in *G. spelaeum* secretion. Gas chromatography and mass spectrometry analyses of secretion taken directly from the glands showed the presence of two components. The major component (ratio about 7:3), which had a molecular ion m/z of 136, was identified as 2-ethyl-1,4-benzoquinone. The other component, a molecular ion m/z of 150, was identified as 2,3,5-trimethyl-1,4-benzoquinone. Moreover, analysis of the mixture taken from live animals detected only water in addition to the two quinones. This means that the enteric fluid contained only water. Therefore, the defensive exudate contains two quinones from the gland mixed with water from the enteric fluid.

Other behavioral defenses.—Individual *Goniosoma* did not shake their body, autotomize their legs, or feign death when handled. If disturbed, *G. spelaeum* tried to escape by running fast and also frequently by dropping from the cave ceiling and remaining motionless for a while to avoid detection. Later they would crawl up the cave walls. The mere approach of an observer often caused the animals to drop. In addition, as already reported for other *Goniosoma* (Bristowe 1925), *G. spelaeum* try to deliver a nip to the offending object by pinching it between their fourth coxae and femora (which seems to be more effective among males because they are more highly armed than females—see Figs. 1–3), sometimes painfully. They always reacted with this behavior when handled near the fourth leg coxae/trochanter articulation. When handled near the oral region, *G. spelaeum* always seized an observer's fingers with its pedipalps and tried to bite with its chelicerae, always harmlessly.

DISCUSSION

External morphology, fluid displacement, and chemical defensive behavior.—The scent glands of *Goniosoma spelaeum* open over coxae II, and are connected by arrangements of channels to the mouth as in other Laniatores (e.g., Eisner et al. 1971; Acosta et

al. 1993). The arrangement in *G. spelaeum* is very similar to that of *Pachyloidellus goliath* (as in figs. 1–3 of Acosta et al. 1993). Although the dorsal apophyses on coxae I and II were considered not to be involved in liquid displacement in *P. goliath* (Acosta et al. 1993), the apophyses on coxae II of *G. spelaeum* are directed towards the gland opening and the larger apophysis (ac^+ of Fig. 4) is placed exactly over the position where ventral channel $c2$ meets the lateral channel. Therefore, it might serve to avoid the overflow of fluid at this sharp turning point. The role of these apophyses in liquid displacement remains to be tested. However, the volume of running fluid is sometimes large and the apophyses might be serving to regulate the upper level preventing overflow.

In the mechanisms of "displacement of the liquid along the lateral area of the scutum" (coded as 2.2. by Acosta et al. 1993) and of "emission of a secretion globule on the gland opening, that is directed to the aggressor with the forelegs" (coded as 3.2.), the chemical substance released by the gland openings may be mixed with oral fluid (basically water, as stated by Eisner et al. 1971) which runs by capillarity in grooves between the anterior coxae to reach the gland opening. Besides our record herein, it has been shown to occur only in *Pachyloidellus goliath* (Acosta et al. 1993), and in all Cosmetidae studied by Eisner et al. (1971, 1977). We should stress that both mechanisms have common steps: first, the enteric fluid from the mouth collects in front of the gland opening; then the secretion is discharged from the gland. At this point, a droplet of mixed fluids is formed in front of the gland opening (which resembles the mechanism of "emission of a secretion globule at the gland opening", coded 1.2., common in some Palpatores and in some Laniatores as well). Afterwards, this droplet may follow the lateral groove as in mechanism 2.2. in *P. goliath*, or be administered by leg dabbing as in mechanism 3.2. in Cosmetidae. Another case with similar (but not all) steps was reported for *Zygopachylus albomarginis* Chamberlin 1925 (Cokendolpher 1987). Although *Z. albomarginis* is listed under the same code 2.2. of Acosta et al. (1993), this species shows two differences from above: the liquid is displaced along a row of tubercles (and not along a lateral groove, as noted by Acosta et al. 1993);

and no droplet is formed in front of the opening; i.e., the secretion oozes from the pore and runs along the lateral margin, and the fluid is then collected distally on a spine forming a droplet (Cokendolpher 1987). This difference in timing of droplet formation was not included in the table from Acosta et al. (1993). In *Goniosoma spelaeum*, a further variation is here registered: the droplet will also be formed distally (always on coxae IV), and not in front of the opening (like in *Z. albomarginis*), but runs through a lateral groove (like in *P. goliath*).

Mixing of glandular secretion with enteric fluid, and its displacement in grooves along the scutum area was reported by Acosta et al. (1993) to be common in Gonyleptidae; at least for Pachylinae, from which several species were morphologically analyzed. In some Gonyleptinae studied, those authors did not find well-defined grooves on the lateral area as they did in Pachylinae. Herein, we noticed the channels pattern in Pachylinae (mouth to gland opening, and towards the body posterior end) also seems to be the rule in Goniosomatinae. However, in the latter the main difference is that there is no droplet formation in front of the gland opening and subsequent running through the groove; i.e., in *Goniosoma* species, the droplet is only formed distally on coxae IV. Moreover, the droplet may or may not contain secretion; and, when it does, the mixture may take place while the enteric fluid runs in front of the opening, or afterwards, when the droplet is already formed. As far as we know, these different timings of mixture were not reported before in harvestmen.

The "emission in form of a fine jet upwards and backwards" (coded as 3.1. by Acosta et al. 1993), which in *G. spelaeum* takes place directly from the gland opening and extends several centimeters in any direction, even forward, has been reported previously only in Triaenonychidae (Lawrence 1938; Maury 1987). However some striking differences were observed. In *Triaenonychoides* spp. the jet might squirt up to 1 cm in distance (Maury 1987) and in *Larifuga capensis* Lawrence 1931 and *Larifugella natalensis* (Lawrence 1931) it extends at least 2.5 cm (Lawrence 1938). In the Triaenonychidae the jet can be emitted only upwards and backwards (Lawrence 1938). However, this author stated that

it might have been due to fixing the animals in such a position that they could not direct the jet, and that it is probable that the animal has some control over the direction in which ejection takes place.

Morphologically, *G. spelaeum* also has secondary outlets at the gland opening region (*ga* and *gp* of Fig. 4). These outlets are probably related to fluid displacement immediately after release from the gland opening, although their function is still not clear. Although, there also seems to be a second opening in *P. goliath* (as in figs. 2, 3 of Acosta et al. 1993), unfortunately those authors did not cite nor comment on it.

Because both the second posterior gland outlet and the powerful jet emitting behavior are first reported herein, we supposed they might be related with each other. Thus, somehow the second opening with its sharp internal projections may be related to the ability of extended jet emission; however, it remains to be tested. Unfortunately, no jet was emitted while studying live animals under a microscope. Therefore, it was not possible to determine the path taken by the secretion. Moreover, when analyzing the illustration of the gland opening in *L. natalensis* (fig. 2b in Lawrence 1938), which also emits a jet, there seem to be two outlets, one anterior and one posterior. Thus, external morphology of the gland opening of jet emitting harvestmen needs further detailed study.

Chemical analysis of exudate.—Fieser & Ardao (1956) stated that, among benzoquinones, some typically show a characteristic yellow color: 2,3-dimethyl-1,4-quinone, 2,5-dimethyl-1,4-quinone, 2,6-dimethyl-1,4-quinone, and 2-ethyl-1,4-quinone. As can be seen in the summary from Acosta et al. (1993), the first is the most common secretion recorded from gonyleptoid harvestmen; the second was detected in two species; and the second most common gonyleptoid compound is 2,3,5-trimethyl-1,4-quinone.

Laboratory analyses of the yellowish chemical exudate of *Goniosoma spelaeum* identified 2-ethyl-1,4-quinone (the fourth in Fieser & Ardao's list given above) as the major component, and 2,3,5-trimethyl-1,4-quinone as the second component. The major compound is here reported for the first time for opilionids. The second is common in several of the Gonyleptidae and Cosmetidae (Laniatores) studied

(see Acosta et al. 1993). It is noteworthy that the latter was never the major component in secretions of the harvestmen from which it was identified (e.g., Eisner et al. 1977).

Other behavioral defenses.—The *Goniosoma spelaeum* behavior of dropping from the ceiling and remaining motionless for a while probably evolved as a defense against epigean predators and has been maintained because these harvestmen inhabit the twilight zone and leave the caves for feeding. This does not constitute feigning death because, if taken from the floor and handled, they tried to escape. The behavior of delivering a nip to the offending object by pinching it between their fourth coxae and femora was also reported for *Acanthopachylus aculeatus*, by Capocasale and Bruno-Trezza (1964), who stated that one is led to release the animals because of the shock, not because this behavior could harm the observer. In contrast, we found that the very sharp armature of *G. spelaeum* was painful, and sometimes caused bleeding. Finally, the common behavior of biting with the chelicerae, although harmless to human skin, may be effective with smaller aggressors.

ACKNOWLEDGMENTS

LITERATURE CITED

Acosta, L.E., T.I. Poretti & P.E. Mascarelli. 1993. The defensive secretions of *Pachyloidellus goliath* (Opiliones, Laniatores, Gonyleptidae). Bonn. zool. Beitr., 44:19–31.

Berland, L. 1949. Ordre des Opilions. Pp. 761–793, *In* Traité de Zoologie, Vol. 6. (P.P. Grassé, ed.). Maisson et Cie., Paris.

Blum, M.S. & A.L. Edgar. 1971. 4-methyl-3-heptanone: Identification and role in opilionid exocrine secretions. Insect Biochem., 1:181–188.

Bristowe, W.S. 1925. Notes on the habits of insects and spiders in Brazil. Trans. R. Entomol. Soc. London, 1924:475–504.

Capocasale, R. & L. Bruno-Trezza. 1964. Biologia de *Acanthopachylus aculeatus* (Kirby, 1819), (Opiliones; Pachylinae). Rev. Soc. Uruguaya Entomol., 6:19–32.

Cokendolpher, J.C. 1987. Observations on the defensive behaviors of a Neotropical Gonyleptidae (Arachnida, Opiliones). Rev. Arachnol., 7:59–63.

Duffield, R.M., O. Olubajo, J.W. Wheeler & W.A. Shear. 1981. Alkylphenols in the defensive secretion of the Nearctic opilionid, *Stygnomma spinifera* (Arachnida: Opiliones). J. Chem. Ecol., 7:445–452.

Edgar, A.L. 1971. Studies on the biology and ecology of Michigan Phalangida (Opiliones). Misc. Publ. Mus. Zool. Univ. Michigan, 144:1–64.

Eisner, T., D. Alsop & J. Meinwald. 1978. Secretions of opilionids, whip scorpions, and pseudoscorpions. Pp. 87–99, *In* Handbook of Experimental Pharmacology, Vol. 48. (S. Bettini, ed.). Springer-Verlag, Berlin.

Eisner, T., T.H. Jones, K. Hicks, R.E. Silberglied & J. Meinwald. 1977. Quinones and phenols in the defensive secretions of neotropical opilionids. J. Chem. Ecol., 3:321–329.

Eisner, T., F. Kluge, J.E. Carrel & J. Meinwald. 1971. Defense of phalangid: Liquid repellent administered by leg dabbing. Science, 173:650–652.

Ekpa, O., J.W. Wheeler, J.C. Cokendolpher & R.M. Duffield. 1984. N,N-dimethyl-β-phenylethylamine and bornyl esters from the harvestman *Sclerobunus robustus* (Arachnida: Opiliones). Tetrahedron Lett., 25:1315–1318.

Ekpa, O., J.W. Wheeler, J.C. Cokendolpher & R.M. Duffield. 1985. Ketones and alcohols in the defensive secretion of *Leiobunum townsendi* Weed and a review of the known exocrine secretions of Palpatores (Arachnida: Opiliones). Comp. Biochem. Physiol., 81B:555–557.

Estable, C., M.I. Ardao, N.P. Brasil & L.F. Fieser. 1955. Gonyleptidine. J. American Chem. Soc., 77:4942.

Fieser, L.F. & M.I. Ardao. 1956. Investigation of the chemical nature of Gonyleptidine. J. American Chem. Soc., 78:774–781.

Gnaspini, P. 1995. Reproduction and postembryonic development of *Goniosoma spelaeum*, a cavernicolous harvestman from southeastern Brazil (Arachnida: Opiliones: Gonyleptidae). Inv. Reprod. Develop., 28:137–151.

Gnaspini, P. 1996. Population ecology of *Gonio-soma spelaeum*, a cavernicolous harvestman from south-eastern Brazil (Arachnida: Opiliones: Gonyleptidae). J. Zool., 239: 417–435.

Hillyard, P.D. & J.H.P. Sankey. 1989. Harvestmen. Synopses of the British Fauna, n.s., 4:1–119.

Jones, T.H., W.E. Conner, A.F. Kluge, T. Eisner & J. Meinwald. 1976. Defensive substances of opilionids. Experientia, 32:1234–1235.

Jones, T.H., J. Meinwald, K. Hicks & T. Eisner. 1977. Characterization and synthesis of volatile compounds from the defensive secretions of some "daddy longlegs" (Arachnida: Opiliones: *Leiobunum* spp.). Proc. Natl. Acad. Sci. USA, 74:419–422.

Juberthie, C. 1961. Structure et fonction des glandes odorantes chez quelques opilions (Arachnida). Zool. Anz. (Suppl.), 25:533–537.

Juberthie, C. 1976. Chemical defence in soil opil-iones. Rev. Écol. Biol. Sol, 13:155–160.

Kaestner, A. 1968. Order Opiliones, Harvestmen. Pp. 229–247, *In* Invertebrate Zoology. Vol. 2. John Wiley & Sons.

Lawrence, R.F. 1938. The odoriferous glands of some South African harvest-spiders. Trans. Roy-al Soc. South Africa, 25:333–342.

Maury, E.A. 1987. Triaenonychidae sud-americanos. IV. El género *Triaenonychoides* H. Soares 1968 (Opiliones, Laniatores). Bol. Soc. Biol. Concepción, 58:95–106.

McLafferty, F.W. & D.B. Stauffer. 1989. The Wiley INBS Registry of Mass Spectral Data. Vol. 1. New York.

Meinwald, J., A.F. Kluge, J.E. Carrel & T. Eisner. 1971. Acyclic ketones in the defensive secretion of a "daddy longlegs" (*Leiobunum vittatum*) (Arachnida/Opiliones). Proc. Natl. Acad. Sci. USA, 68:1467–1468.

Roach, B., T. Eisner & J. Meinwald. 1980. Defen-sive substances of opilionids. J. Chem. Ecol., 6: 511–516.

Wiemer, D.F., K. Hicks, J. Meinwald & T. Eisner. 1978. Naphthoquinones in defensive secretion of an opilionid. Experientia, 34:969–970.

THE WEB OF *NUCTENEA SCLOPETARIA* (ARANEAE, ARANEIDAE): RELATIONSHIP BETWEEN BODY SIZE AND WEB DESIGN

Astrid M. Heiling[1] and Marie Elisabeth Herberstein[1,2]: [1]Institute of Zoology, University of Vienna, Althanstr. 14, A- 1090 Vienna, Austria; and [2]Department of Zoology, University of Melbourne, Parkville Victoria 3052, Australia

ABSTRACT. The relationship between body size and web design was studied for the nocturnal orb-weaving spider *Nuctenea sclopetaria*. Body measurements (carapace width, leg length, body length and wet weight) taken from 27 adult female and 22 juvenile spiders were related to web dimensions (capture area, number of radii, capture thread length, mesh height) each spider constructed. Carapace width was found to be the most reliable size measure for predicting web dimensions for adult and juvenile spiders. The study also found that the webs showed a distinct asymmetry due to the enlargement of the lower web half and the extent of this asymmetry increased with carapace width. Furthermore, mesh height increased with distance from the hub. The possible effects of web asymmetry on the prey capture success of spiders are discussed.

The webs of orb-web weaving spiders show great variations in their specific designs (see Eberhard 1986 for a summary) which have been interpreted as specializations for the capture of specific prey types (e.g., Eberhard 1980, 1986; Brown 1981; Murakami 1983; Craig 1987b, c; Walker 1992; Rhisiart & Vollrath 1993; Miyashita & Shinkai 1995). Orb web design can also vary between individuals of the same species and even within individuals in response to prey size (Sandoval 1994), food availability, egg production (Sherman 1994), web site and spider size (Eberhard 1988). Within species, web design (e.g., web size and mesh size) can relate to various measures of body size such as spider length (Waldorf 1976; Brown 1981), carapace width (Olive 1980; Murakami 1983; Eberhard 1988), leg length and spider weight (Eberhard 1988) but other studies have not found such relationship between spider size and web design (Leborgne & Pasquet 1987). Similarly, not all body dimensions may be equally relevant to web design. The body size of spiders can change quite drastically within a short period of time during the ingestion of large prey and during a molt (Vollrath & Köhler 1996). While the accumulation of energy reserves through foraging influences the molt and the increase in body size after the molt, prey ingestion also affects body weight immediately

and directly (Vollrath 1987a). Thus, spider weight is also an indicator of the spider's satiation level that directly influences web investment and consequently web design (Sherman 1994).

Furthermore, in an adult spider that has undergone its final molt, spider weight reflects the recent foraging success as well as the cumulative foraging success between molts. In contrast, body size characteristics such as leg length or carapace size reflect the foraging success prior to the final molt but are no longer influenced by the prey captured after the final molt (Vollrath 1987a; 1988). Leg length can also be misleading as autonomized legs regenerate shorter than normal legs (Vollrath 1987b). Consequently, various body size measures may have different significance in relation to web design depending on whether the spider is juvenile and still undergoing molts or whether it is adult. In addition to inter- and intraspecific differences in web design, webs are not necessarily symmetrical, and various web elements can be differentially allocated in the top half compared to the bottom half of the web. An example of such web asymmetry is the ladder web built by *Kryptaraneus atrihastulus* (Urquhart 1891) with extreme up or down extensions of the orb (Forster & Forster 1985).

The objective of the present study is to de-

scribe the variation of orb web design, using the webs of *Nuctenea sclopetaria* (Clerck 1757). This species of nocturnal orb weavers is common in urban habitats and often found in high densities near water (Wasowska 1973). By relating a number of different body size measures to various web characteristics we aim to identify useful size measures for both adult and juvenile spiders and to describe the relationship between spider size and web design in comparison with previous studies. Furthermore, we describe the nature of web asymmetry in this species and reveal how various web elements are differentially allocated. Voucher specimens of this species were deposited in the Arachnoidea collection at the Natural History Museum, Vienna, Austria.

METHODS

The material for this study was collected from a footbridge (length = 59 m) across the Danubian Channel in the 9th Vienna district, Austria. *Nuctenea sclopetaria* builds webs near the fluorescent lighting tubes affixed to the top of the handrails (height = 1.31 m) on the footbridge. Observations were made from July until late September 1995, in the evening, after the lights had been switched on. The 27 adult female and 22 spiders (of unidentifiable sex) were selected randomly, and their web and body dimensions were examined. Spiders were removed from their webs and taken to the laboratory where they were weighed to the nearest 0.1 mg on an electronic balance. Carapace width, body length and length of the first right leg (tarsus to coxa) were measured to the nearest 0.01 mm, using a binocular microscope equipped with a Wild Censor.

After the removal of spiders, webs were sprayed with a fine mist of water (Stowe 1978) and cornstarch (Carico 1977) to improve resolution, backlit and photographed using high contrast black and white film. All web parameters were measured directly from these photographs. On the web surface with a clockwise oriented capture spiral, the northern and southern cardinal sectors were defined as the vertically directed sectors above and below the hub, respectively and the eastern and western cardinal sectors were defined as the horizontally directed sectors on the right and on the left hand side of the hub, respectively (Fig. 1). The total capture thread length, as a measure of web investment was obtained by

tracing and measuring the length of each spiral thread in the web. The total area covered by the sticky spirals (capture area) was calculated using various web parameters. The total number of radii in the web was counted. The number of capture thread rounds and the length of each radius were obtained for each of the cardinal sectors (north, east, south and west; see Fig. 1). The average mesh height in the webs was calculated from the distances between the capture threads in the vertical directed sectors. Each distance between the spirals in the southern-directed sector of the web (Fig. 1) was also measured in relation to its distance to the hub.

Statistical analyses.—As all data were normally distributed (Kolmogorov-Smirnov), parametric tests were applied. The relationships of all body size measures (carapace width, leg length, body length and wet weight) to capture thread length, number of radii, mesh height and capture area were calculated using Pearson correlations, treating adult females and juveniles separately. To investigate the asymmetric nature of the webs built by adult female spiders, radii length and number of capture threads were compared between the eastern and western sector as well as between the northern and southern sectors using paired *t*-tests as web measures were not independent. The differences between the upper and lower web halves (northern and southern sectors) were further analyzed comparing the capture thread length, the number of radii, the mesh height and the capture area (Fig. 1) using paired *t*-tests.

Web asymmetry was defined as the absolute difference in the number of capture thread rounds between the upper and lower vertical radius. It was related to spider size using regression analysis, pooling the data of adult female and juvenile webs. The relationship between mesh height measured in the southern sector (Fig. 1) and the distance from the hub to the relating mesh in the webs of adult females was investigated using Spearman rank correlations.

RESULTS

In adult females, capture area increased significantly with carapace width and capture thread length increased significantly with carapace width and wet weight, while leg length and body length did not relate to these two
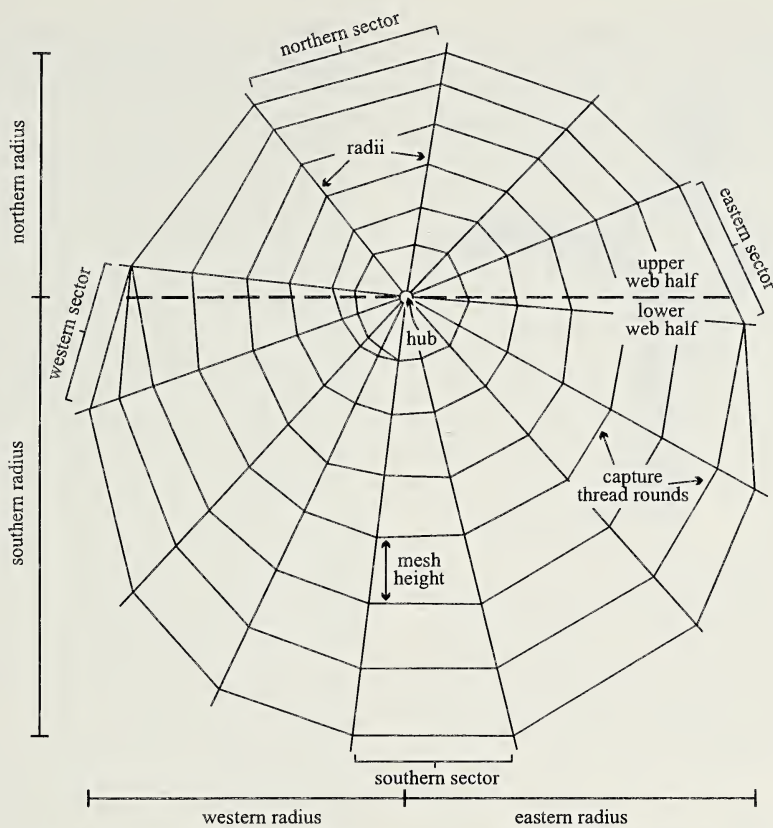
Figure 1.—Schematic orb web, representing the measured parameters.

web variables (Table 1). The number of radii and the mesh height in the webs of adults females did not correlate with any of the four different body size measures of the spiders. In contrast, all body measures, taken from juveniles, were significantly positively correlated with capture thread length, capture area and mesh height (Table 1). As for the webs of adult spiders, there was also no correlation between any of the body measures and the number of radii in the webs of juveniles (Table 1)

and the mean ($\pm$ SD) number of radii did not differ between the webs of adult females (18 $\pm$ 2.2) and juveniles (17.9 $\pm$ 2.7).

The comparison of the number of capture thread rounds and radii length in the four cardinal sectors of the webs (Fig. 2) revealed that the eastern and western sectors did not differ significantly ($t = -0.73$, $df = 26$, $P > 0.05$; $t = -0.42$, $df = 26$, $P > 0.05$, respectively), but the northern and southern sectors did (number of capture thread rounds: $t = -9.06$,

Table 1.—The correlation coefficients (r) for body- and web measures of adult female ($n = 29$) and juvenile ($n = 22$) *Nuctenea sclopetaria* (* $P < 0.05$; ** $P < 0.01$).

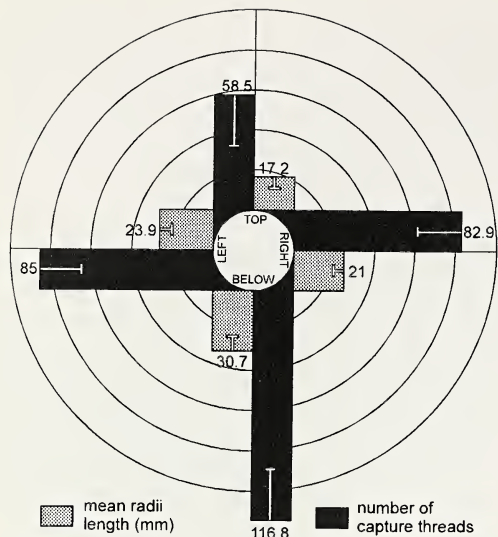|	Capture area (mm²)		Capture thread length (mm)		Number of radii		Mesh height (mm)	
	Female	Juvenile	Female	Juvenile	Female	Juvenile	Female	Juvenile
Carapace width	0.48**	0.8**	0.42*	0.68**	0.03	−0.12	0.15	0.61**
Leg length	0.29	0.7**	0.36	0.63**	0.03	−0.19	0.064	0.53**
Body length	−0.08	0.66**	0.03	0.58**	0.07	−0.21	−0.23	0.48*
Wet weight	0.25	0.74**	0.38*	0.62**	0.06	−0.09	−0.02	0.47*

Figure 2.—Mean radii length from the hub to the outermost spiral (mm, black bars), and number of capture threads (gray bars) in the four cardinal directions in webs of adult female *Nuctenea sclopetaria*. Only one SD bar was drawn to simplify the graph. Interval of concentric lines: 20 mm or 20 capture threads, respectively ($n = 27$).

$df = 26$, $P < 0.001$; radii lengths: $t = -11.9$, $df = 26$, $P < 0.001$). Comparisons of more web elements between the upper (northern) and lower (southern) web half revealed further differences. The lower web half contains a significantly longer capture thread, significantly more radii and has a significantly larger capture area than the upper web half (Table 2).

The degree of web asymmetry, defined as the absolute difference in the number of capture thread rounds between the northern and the southern radius, was not constant. It increased significantly with carapace width ($y = 0.982 \times 10^{(0.24x)}$; $R^2 = 0.374$, $df = 47$, $P < 0.001$). Similarly, the distances between the capture spirals (measured in the southern sec-

tor only) were also not constant throughout the sector, but increased significantly with distance from the hub ($r = 0.6735$, $df = 26$; $P < 0.001$).

DISCUSSION

The web design in adult spiders related differently to the various body size measures. Only capture area and capture thread length increased with carapace width, in accordance with previous studies that also found a positive relationship between carapace width and web size (Olive 1980; Murakami 1983; Eberhard 1988). Interestingly, capture thread length also increased with spider weight. This is surprising, as heavier spiders are presumably more satiated or close to producing a cocoon and are thus expected to decrease their foraging effort expressed by capture thread length (Sherman 1994). It may be that in our spiders wet weight reflected the overall size of the spider more accurately and not so much the recent prey ingestion and thus satiation.

Mesh height did not relate to any of the body size measures for adult spiders, contrasting the results other studies that found leg length a good indicator of mesh height (Vollrath 1987b; Eberhard 1988). However, mesh height can be variable and spiders may alter it independent of spider size to target specifically sized prey (Sandoval 1994). The prey captured by the population of *N. sclopetaria* in our study almost exclusively consisted of small (2.7 ± 0.7 mm body length) chironomid flies, and the mesh height in their webs may be more related to the available prey size than leg length. In contrast to adult spiders, capture area, capture thread length and mesh height related to all body size measures of juvenile spiders, suggesting that size in juveniles has different impacts on web design compared to adults. Consequently, for comparisons between adults and juveniles, carapace width

Table 2.—Web characteristics of adult female *Nuctenea sclopetaria*. Capture thread length, number of radii and capture area differed significantly between the upper and the lower web half. All figures are Mean ± SD ($n = 27$; *** $P < 0.001$).

	Upper web half	Lower web half	t
Capture thread length (mm)	3944 ± 1389	7524 ± 1905	12.88***
Number of radii	7.7 ± 1.1	10.3 ± 1.6	7.59***
Capture area (mm²)	14 680 ± 5760	26 676 ± 9141	10.34***

seems to be the most appropriate variable to indicate the effect of body size on web design.

The number of radii in the web did not correlate with body size in either adult or juvenile spiders. This pattern could be attributed to a number of causes. Non-sticky radii function to stabilize the orb-web; and, consequently, there may be a minimum number of radii necessary for web construction. Radii-rich webs have also been shown to absorb more kinetic energy and are therefore proposed as adaptations to heavier and/or faster flying prey (Craig 1987a; Eberhard 1990). Additionally, larger spiders may increase web stability by increasing the diameter of their silk as an isometric function of spider size (Craig 1987a), rather than by constructing more radii.

The present results reveal a very characteristic asymmetry in the webs of adult female *N. sclopetaria*. While the left and right sides of the web are similar, significantly more material was invested in the lower web half than in the upper half. Like most orb-web spiders, *N. sclopetaria* starts attacking prey from the hub of the web, hanging head downwards. By placing the hub above the center of the web, prey capture success of *N. sclopetaria* can be enhanced, as the time taken to reach prey entangled in the lower half is shorter than in the upper one (Masters & Moffat 1983). Similarly, by hanging head downwards the spider locates prey in the lower half of the web faster than in the upper half (Klärner & Barth 1982) which may lead to an increased prey capture success. Consequently, there may be a selection for asymmetric webs with an emphasis on the lower web half in vertical orb-webs.

Interestingly, web asymmetry increased with body size. Whereas there is room for variation in web design that can change within an individual nightly (Sherman 1994), the general web architecture is thought to be genetically determined and therefore not influenced by individual experience (Foelix 1992). Therefore, web asymmetry may be an indicator for changes in web structure due to previous experience, which in turn increases prey capture success.

Nuctenea sclopetaria places the capture spiral in a way that the distance between consecutive spirals (mesh height) increases significantly with distance from the hub. This may reflect a strategy to optimize the prey capture efficiency of the web. The closer to the hub

the prey is retained, the faster it can be reached and subdued by the spider. If the prey is entangled further from the hub, it may have a higher chance of escape (Rhisiart & Vollrath 1993). Consequently, the capture threads near the hub are most important and thus the investment of sticky material should decrease with increasing distance from the hub. This phenomenon has already been observed for the webs of *Araneus diadematus* (Clerck 1757) (Nentwig 1983; Vollrath 1987). The present study found carapace width to be the most reliable predictor of web dimensions for adult and juvenile *Nuctenea sclopetaria* and supports the use of carapace width in future studies concerned with relationship of body size to web dimensions.

LITERATURE CITED

Brown, K.M. 1981. Foraging ecology and niche partitioning in orb-weaving spiders. Oecologia, 50:380–385.

Carico, J.E. 1977. A simple dusting device for coating orb webs for field photography. Bull. British Arachnol. Soc., 4:100.

Craig, C.L. 1987a. The ecological and evolutionary interdependence between web architecture and web silk spun by orb weaving spiders. Bio. J. Linn. Soc., 30:135–162.

Craig, C.L. 1987b. Alternative foraging modes of orb web weaving spiders. Biotropica, 21:257–264.

Craig, C.L. 1987c. The significance of spider size to the diversification of spider-web architectures and spider reproductive modes. American Nat., 129:47–68.

Eberhard, W.G. 1980. Spider and fly play cat and mouse. Nat. Hist., 89:56–60.

Eberhard, W.G. 1986. Effects of orb-web geometry on prey interception and retention. Pp. 71–100, *In* Spiders: Webs, Behavior and Evolution (W.A. Shear, ed). Stanford Univ. Press, Stanford, California.

Eberhard, W.G. 1988. Behavioral flexibility in orb web construction: effects of supplies in different silk glands and spider size and weight. J. Arachnol., 16:295–302.

Eberhard, W.G. 1990. Function and phylogeny of spider webs. Ann. Rev. Ecol. Syst., 21:341–372.

Foelix, R.F. 1992. Biologie der Spinnen. Thieme, Stuttgart, Germany.

Forster, L.M. & R.R. Forster. 1985. A derivative of the orb web and its evolutionary significance. New Zealand J. Zool., 12:455–465.

Higgins, L.E. 1990. Variation in foraging investment during the intermolt interval and before egg-laying in the spider *Nephila clavipes* (Araneae: Araneidae). J. Insect. Behav., 3:773–783.

Klärner, D. & F.G. Barth. 1982. Vibratory signals and prey capture in orb-weaving spiders (*Zygiella x-notata*, *Nephila clavipes*; Araneidae). J. Comp. Physiol., 148:445–455.

Leborgne, R. & A. Pasquet. 1987. Influences of aggregative behaviour on space occupation in the spider *Zygiella x-notata* (Clerck). Behav. Ecol. Sociobiol., 20:203–208.

Masters, W. &. A.J.M. Moffat. 1983. A functional explanation of top-bottom asymmetry in vertical orb web. Anim. Behav., 31:1043–1046.

Miyashita, T. & A. Shinkai. 1995. Design and prey capture ability of webs of the spiders *Nephila clavata* and *Argiope bruennichii*. Acta Arachnol., 44:3–10.

Murakami, Y. 1983. Factors determining the prey size of the orb-web spider, *Argiope amoena* (L. Koch) (Argiopidae). Oecologia, 57:72–77.

Nentwig, W. 1983. The non-filter function of orb webs in spiders. Oecologia, 58:418–420.

Olive, C.W. 1980. Foraging specializations in orb-weaving spiders. Ecology, 61:1133–1144.

Rhisiart, A. & F. Vollrath. 1993. Design features of the orb web of the spider, *Araneus diadematus*. Behav. Ecol., 5:280–287.

Sandoval, C.P. 1994. Plasticity in web design in the spider *Parawixia bistriata*: a response to variable prey type. Funct. Ecol., 8:701–707.

Sherman, P.M. 1994. The orb-web: an energetic and behavioural estimator of a spider's dynamic foraging and reproductive success. Anim. Behav., 48:19–34.

Stowe, M.K. 1978. Observations of two nocturnal orb weavers that build specialized webs: *Scoloderus cordatus* and *Wixia ectypa* (Araneae: Araneidae). J. Arachnol., 6:141–146.

Vollrath, F. 1987a. Growth, foraging and reproductive success. Pp. 357–370, *In* Ecophysiology of spiders. (W. Nentwig, ed). Springer Verlag, Berlin.

Vollrath, F. 1987b. Altered geometry of webs in spiders with regenerated legs. Nature, 328:247–248.

Vollrath, F. 1988. Spider growth as an indicator of habitat quality. Bull. British Arachnol. Soc., 7:217–219.

Vollrath, F. & T. Köhler. 1996. Mechanics of silk produced by loaded spiders. Proc. R. Soc. London (B), 263:387–391.

Waldorf, E.S. 1976. Spider size, microhabitat selection and use of food. American Nat., 96:77–87.

Walker, J.R. 1992. What do orb webs catch? Bull. British Arachnol. Soc., 9:95–98.

Wasowska, S. 1973. The variability of the number of external spinning structures within one population of *Araneus sclopetarius* Clerck. Zool. Poloniae, 23:109–118.

DISPERSAL IN THE SOLITARY *STEGODYPHUS AFRICANUS* AND HETEROSPECIFIC GROUPING WITH THE SOCIAL *STEGODYPHUS DUMICOLA* (ARANEAE, ERESIDAE)

U. Seibt, I. Wickler and **W. Wickler**: Max-Planck-Institut für Verhaltensphysiologie; D-82319 Seewiesen, Federal Republic of Germany

ABSTRACT. Mobility and dispersal of the solitary-living spider, *Stegodyphus africanus* Blackwall 1866, under laboratory conditions are described for the period from four months after hatching until death. Cohabitation with females of the social-living *S. dumicola* Pocock 1898, within the same experimental setup, reveals interspecific tolerance between both species.

Special attention has recently been paid to the cribellate eresid spider genus *Stegodyphus* Simon 1892 which contains both subsocial species with solitary adults, hereafter referred to as solitary, as well as permanently social species. A revision of the genus by O. & M. Kraus (1988) suggests three monophyletic subtaxa, or species groups, each of which includes a number of solitary as well as a single social species, proposing that sociality evolved independently three times. In view of the socially intolerant and aggressive lifestyle of the vast majority of spiders, the permanently and cooperatively social (Wickler & Seibt 1993) species form noteworthy exceptions. Unfortunately, up to now the biology of the social species' solitary sister species is practically unknown. On *S. africanus* in particular, nothing had been published except for the original description in 1866.

In Krüger Park, South Africa and in Swaziland we repeatedly found a fully-grown *S. africanus* female living parasitically in a colony of the social *S. dumicola* and even consuming individuals of the host species (Wickler & Seibt 1988). Therefore, we also wanted to confront the *S. africanus* under controlled laboratory conditions with *S. dumicola*, hoping for more data on interspecific behavior.

METHODS

In February 1992, near Nshawu-Dam in the Krüger Park (South Africa, Transvaal; 23°29′S, 31°29′E) in dry, fairly flat grassland with squat *Colophospermum mopane* trees, we collected a *S. africanus* silk nest, 8 cm in diameter, situated about two meters high in a mopane bush, containing a dead adult female with 82 living spiderlings, of 3–4 mm body length (= prosoma + opisthosoma, measured to ± 0.1 mm with a vernier calliper). We took the sponge-like nest to our laboratory to obtain data on the dispersal tendency of the growing spiderlings. Voucher specimens have been deposited in the arachnid collection of the Zoological Museum, Hamburg University.

We estimated that the *S. africanus* spiderlings had hatched from the cocoon at the beginning of January, about 30 days prior to collection. Four months after hatching, we placed the original nest with 54 surviving spiderlings into a 12-sided acrylic plastic (Plexiglas™) container (Fig. 1) with a removable wire screen area in the floor for aeration, feeding and cleaning. Along the outer rim of the container's flat ceiling, 12 evenly spaced "houses" served as housing for emigrants; they consisted of a vertical Plexiglas "pipe" (C) which opened into a larger compartment, a Plexiglas cylinder (D) with a removable wire screen lid. The spiders were fed mostly flies, according to their sizes; and food was simultaneously supplied to all of them at their respective sites in order not to enforce feeding migrations and accumulations.

Within the Plexiglas container we identified 49 sites (see Fig.1): Twelve A, B, C, D locations, plus the central ground area where the original nest had been placed. At variable intervals (one day or more) we recorded the numbers of spider sightings at those sites (i.e., outside the original nest) starting on 29 April 1992. The observed number of animals varied because some returned to their non-transparent home nest or died.
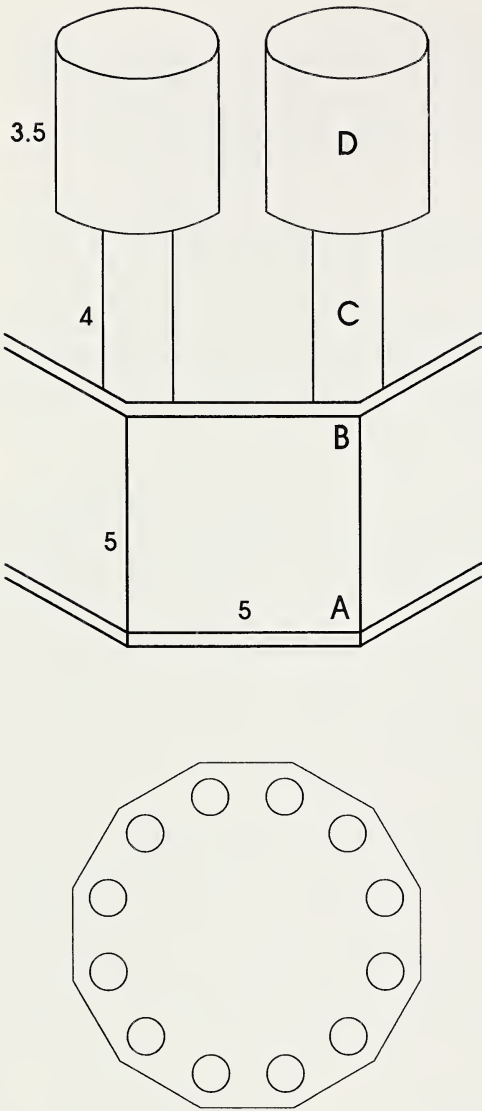
Figure 1.—Diagram of the acrylic plastic (Plexiglas™) apparatus (diameter = 19 cm): Face of one side with two of the twelve "houses": A, B, C, D, observation sites; numbers, lengths in cm. Below: Cross-section at level C.

Table 1.—Observation periods and *Stegodyphus* spiders observed.

Species	Period	Days per period	Proto-cols per period	Spiders (n)	Sightings (n)
S. africanus	I	59	28	36	851
S. africanus	IIa	113	23	32	430
S. africanus	IIb	82	10	8	79
S. africanus	III	207	68	8	244
S. dumicola				21	406

moved. In our system, these spiders turned up elsewhere; an increase of spider number at a given site from first to second record was therefore ignored.

The total observation time (461 days) was formally subdivided into three periods (Table 1): Period IIa began when the first adult *S. africanus* males appeared, and it ended when the last *S. africanus* male had died and only female *S. africanus* were left (Period IIb). Period III began when we added *S. dumicola* individuals from a colony that we had collected in December 1992 near the *S. africanus* locality. Thus, periods I and II deal with *S. africanus* only, while during period III the two species are mixed.

Young *Stegodyphus* tend to stay in the maternal web structure until a certain age, at which they begin to disperse. In our experimental setup spiders had the option to disperse, and to form groups or isolate themselves; we always found some (though different) "houses" empty (from 1–3 in period IIa to 2–7 in period III, with always 13–30 spiders present).

RESULTS AND DISCUSSION

On 28 April 1992 the *S. africanus* spiderlings had grown to a body length between 4.0–7.5 mm (mean $\bar{X} = 5.4$, SD = ± 0.8 mm; $n = 54$); their weight ranged from 7–49 mg. About four months later, adult males measured from 4–12 mm (8.3 ± 1.6 mm; $n = 20$) and weighed from 48–170 mg (73.8 ± 41 mg; $n = 18$). At the same time females measured from 8.4–16.0 mm (12.2 ± 2.5 mm; $n = 17$) and weighed from 79–545 mg (370 ± 210 mg; $n = 24$). As indicated by field data (Seibt & Wickler 1988), fully grown social *S. dumicola* females are much smaller (7.5 ± 1.2

As numbers of spiders per site varied between records, pairs of records 24 h apart were chosen to estimate spider mobility. Due to ongoing asynchronous moltings, the individuals could not be marked without destructive interference. Therefore, we assumed no mobility if the number of spiders at a given site had not changed between successive records. A lower count in a second record gave the minimum number of spiders that had
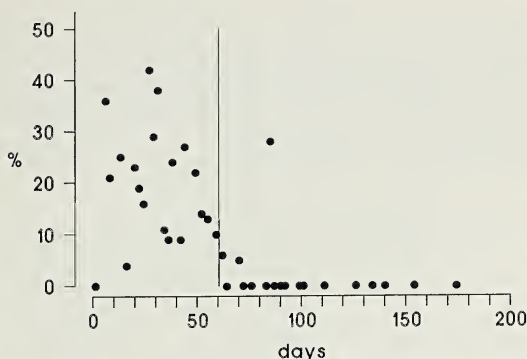
Figure 2.—Percent of recorded spiders in the ground region in 38 (independent) protocols over 173 days. The vertical line separates periods I and IIa.

mm, $n = 877$; 49.1 ± 2.5 mg, $n = 848$) than *S. africanus*.

In our apparatus, we found 24 young outside the maternal nest on the first observation day, 28 on the 8th, 36 on the 27th day. Many of them tended to stay within the ground region, i.e., next to the maternal nest. In order to test for independent data, an autocorrelation was run between successive protocols. We pooled all sites A and the central ground area into "ground region", and 12 times sites B, C, D into 12 house-regions. Autocorrelation analysis then left us with independent data from 20 protocols in Period I and 18 in Period IIa. No individual was found in the ground region in just one protocol in period I, but in period IIa, they were there in 15 protocols. The difference is significant ($P < 0.001$, $\chi^2 = 20.7$, $df = 1$). This change in preference for the upper regions B, C and D coincides with the appearance of the first adult male on observation-day 61 (Fig. 2). Thereafter the home nest was no longer used. Spider sightings from the available 12 house-regions during all periods deviated significantly from uniformity. But no consistent preferences for specific house-regions over periods I and IIa were found.

During period I, *S. africanus* spiders formed close contact groups of up to 15 conspecifics in 66% of all sightings ($n = 851$); in 34% they were seen singly. As long as males were present (up to 12 in period IIa), female spiders formed groups of maximally 5 females in 42% of 354 sightings, in 58% they were seen singly. After the males died (period IIb),

females were seen pairwise in 10% of all sightings ($n = 79$), in 90% singly. The difference between periods IIa and IIb is significant ($P < 0.001$, $\chi^2 = 27$, $df = 1$). This decreasing number of grouped animals over time could be due to an effect of male presence, of decreasing numbers, or of increasing age. As 58% of a total of 129 male sightings showed them without females, males do not seem to attract females or induce female groupings. To account for the decrease in number of animals and increasing age over time, a partial correlation was used: a series of 61 protocols over the successive periods I, IIa and IIb showed a significant ($P < 0.05$; two-tailed, partial correlation coefficient = 0.31) age dependent increase in percent of animals seen isolated *vs.* grouped, proving an increase in isolation tendency with age. *S. dumicola* females formed close contact groups with up to 13 conspecifics in 77% of all 406 sightings (Table 1, period III). The grouping tendency was therefore most like that of *S. africanus* spiderlings.

In 49% of all protocols for periods II and III we found a single *S. africanus* in a previously unoccupied "house", proving that spiders did not just move between groups. In 21 of 24 cases where between two successive records only one spider had moved from one site to another it had covered the distances between 2, 3 or 4 "houses". We found no difference in the total rate of site-changes within 24 hours between *S. africanus* spiderlings (105 changes in 286 sightings in Period I) and females (24 changes in 65 sightings in Period IIa) ($R*C$ test, $P = 0.91$, $\chi^2 = 0.012$, $df = 1$). The available settlement areas ("houses") were homogeneously designed, and there were no consistent preferences by the spiders for any one of them. Mobility of the spiders decreased over time, most likely as the individuals settled in separate nest tubes, as they would do in the field. Fully grown *S. dumicola* females (Period III) had changed location between records 24 hours apart in 41 of 86 sightings. There is no significant difference to *S. africanus* spiderlings (105 changes in 286 sightings, period I) ($P = 0.09$, $\chi^2 = 2.89$, $df = 1$) and females (24 changes in 65 sightings, period IIa) ($P = 0.25$, $\chi^2 = 1.3$, $df = 1$).

During period III the apparatus contained females of *S. africanus* and *S. dumicola*. In 69 cases females of both species were seen at the

same site, often even in body contact; 66 times there was a single *S. africanus* together with 1–5 *S. dumicola* individuals, and in three instances two *S. africanus* were found with 1–2 *S. dumicola*. Some of these heterospecific groupings lasted up to 18 consecutive days. In 12 cases we recorded which species came to meet the other at a given site; seven times it was *S. dumicola*, three times *S. africanus*, and two times females of both species met at a new site. In 13 cases (when twice as many *S. dumicola* than *S. africanus* females had been present) we recorded which species ended the heterospecific grouping; 10 times it was *S. dumicola*, two times *S. africanus*, and once all females separated. These results show that females of neither species avoid those of the other species. In the field we have found both sexes of *S. africanus* living in a *S. dumicola* nest. Thus, interspecific tolerance does not seem to be confined to the female sex.

No hostile or cannibalistic behavior between species was observed in the experimental setup. Such interspecific tolerance may be governed by a simple cost/benefit assessment, with the cost factor being most important for the socially-living animal. While even large prey as well as aggressive hymenoptera ensnared in the cribellate silk are attacked, the situation is very different with a congeneric spider that does not become ensnared and moves freely. Here attack will provoke counterattack, and the full risk of being severely damaged would fall upon the assailant, while costs arising from tolerance would be shared among all community members (Seibt & Wickler 1988). An alleged alternative explanation, "that the solitary spiders are much larger than the social ones, so that the costs of being aggressive are rather small for *S. africanus* but high for *S. dumicola*" (Schneider 1995) in fact uses the same cost/benefit ar-

gument; but it neglects the high number of *S. dumicola* spiders present in a nest. If many or all of them attacked simultaneously, they could defeat a larger *S. africanus*; but any *S. dumicola* not participating in a group attack saves risks and energy and thus does better.

LITERATURE CITED

Blackwell, J. 1866. A list of spiders captured in the southeast region of Equatorial Africa, with descriptions of such species as appear new to arachnologists. Ann. Mag. Natur. Hist., 18:451–468.

Kraus, O. & M. Kraus. 1988. The genus *Stegodyphus* (Arachnida, Araneae). Sibling species, species groups, and parallel origin of social living. Verh. naturwiss. Ver. Hamburg NF, 30:151–254.

Kraus, O. & M. Kraus. 1990. The genus *Stegodyphus*: systematics, biogeography, and sociality (Araneida, Eresidae). Acta Zool. Fennica, 190:223–228.

Schneider, J. 1995. Survival and growth in groups of a subsocial spider (*Stegodyphus lineatus*). Insect. Soc., 42:237–248.

Seibt, U. & W. Wickler. 1988. Bionomics and social structure of "family spiders" of the genus *Stegodyphus*, with special reference to the African species *S. dumicola* and *S. mimosarum* (Araneida, Eresidae). Verh. naturwiss. Ver. Hamburg NF, 30:255–303.

Wickler, W. & U. Seibt. 1988. Two species of *Stegodyphus* spiders as solitary parasites in social *S. dumicola* colonies (Araneida, Eresidae). Verh. naturwiss. Ver. Hamburg NF, 30:311–317.

Wickler, W. & U. Seibt. 1993. Pedogenetic sociogenesis via the "sibling-route" and some consequences for *Stegodyphus* spiders. Ethology, 95:1–18.

STABILIMENTUM-DECORATED WEBS SPUN BY *CYCLOSA CONICA* (ARANEAE, ARANEIDAE) TRAPPED MORE INSECTS THAN UNDECORATED WEBS

I-Min Tso[1]:   Museum of Zoology and Department of Biology, University of Michigan, Ann Arbor, Michigan USA

ABSTRACT.   In this field study, I tested the insect-attraction hypothesis as one of the functions of stabilimenta spun by *Cyclosa conica* (Pallas 1772) by examining: (1) if stabilimentum-decorated webs trapped more insects, (2) if a larger web diameter was responsible for the higher insect-trapping rate in decorated webs and, (3) if the differential distribution of insects in spiders' habitats was responsible for the higher insect interception rates of decorated webs. The number of wrapped prey, web diameters and presence of stabilimenta was recorded daily from 13 web locations. The stabilimentum-decorated webs of *C. conica* trapped significantly more insects (150% more) than undecorated webs, but they had significantly smaller mean web diameter (19% smaller). Among web locations, there was no significant difference in their insect interception rates, whether the data were collected from decorated or undecorated webs. These results suggest that the higher insect-trapping efficiency of decorated webs spun by *C. conica* resulted from the presence of stabilimenta, instead of from larger web diameters or differential distribution of insects.

Stabilimenta are silky structures on the webs of some diurnal orb-weaving spiders. At least 17 genera of ecribellate and cribellate orb-weavers build various forms of stabilimenta (Eberhard 1990). In most of the genera, stabilimenta are made up entirely of bands of silk that either encircle the hub (e.g., *Lubinella morobensis* Opell 1984 and *Philoponella* sp., see Lubin 1986) or are located at various positions around the hub (e.g., all *Argiope* species, see Levi 1983). Some spiders also incorporate egg sacs, prey remains and/or detritus into the silk bands (e.g., *Cyclosa octotuberculata* Karsch 1879, see Yaginuma 1986), which make the spiders difficult to detect among those objects.

The function of silk stabilimenta have long been a focus of study for arachnologists. For those genera that incorporate other objects into the silk bands, the function of stabilimenta has generally been hypothesized as camouflaging (Eberhard 1973). As to the silk stabilimenta, ever since Simon introduced this term in 1895 suggesting a web-stabilizing function (Robinson & Robinson 1970), many functional hypotheses have been proposed and tested (Nentwig & Heimer 1987; Nentwig &

Rogg 1988; Eberhard 1990). Most of the functional studies on silk stabilimenta have focused on *Argiope* species, which spin linear silk bands arranged either vertically (e.g., *A. aurantia* (Lucas 1833) and *A. trifasciata* (Forskal 1775)) or diagonally (e.g., *A. argentata* (Fabricius 1775)) around the hub (Levi 1983). Investigators have proposed and tested many hypotheses about stabilimenta's possible functions, such as web advertisement, predator defense, web tension adjustment and product under stress (see review in Nentwig & Rogg 1988; Eberhard 1990; Schoener & Spiller 1992 and Kerr 1993).

Recently, insect-attraction has been demonstrated to be one of the functions of *Argiope* spiders' silk stabilimenta. Diagonally arranged silk stabilimenta of *Argiope argentata* were found to reflect ultraviolet-light, and the stabilimentum-decorated webs of those spiders intercepted more insects than undecorated webs (Craig & Bernard 1990; Craig 1991). The webs of *Argiope trifasciata* decorated with vertically-arranged stabilimenta were also found to trap more insects than undecorated webs (Tso 1996). These findings lead me to hypothesize that insect-attraction may also be one of the functions of the silk stabilimenta built by other orb-weaving spiders, such as *Cyclosa* species. The functions of the linear

[1]Current address: Dept. of Biology, Tunghai University, Taichung 407, Taiwan, R.O.C.

stabilimenta build by *Cyclosa* species have not been investigated. Although Rovner (1976) studied how the position of silk stabilimenta and gravity affect wrapped prey placement on the web of *Cyclosa turbinata* (Walckenaer 1841), he did not provide answers regarding the possible functions of the silk stabilimenta of those spiders. To determine the insect attraction ability of *Cyclosa* stabilimenta, I conducted a field study examining whether or not the presence of silk stabilimenta increases the insect-interception of webs spun by *Cyclosa conica* (Pallas 1772).

METHODS

Cyclosa conica (see Levi 1977) builds webs between dry tree branches in the dim forest understory. Only adult female spiders were used in this study since mature males *C. conica* do not build as full a web as did females (Kaston 1948). Sometimes spiders added a stabilimentum made of white silk band on their webs, making the webs relatively easy to be located by researchers. *Cyclosa conica* have been reported to load the stabilimentum with prey pellets, plant detritus or, in subsequent webs, egg sacs (Comstock 1913; Marples & Marples 1937). However, the *C. conica* population at this study site seldom retained the old stabilimenta. Instead, for all the spiders, stabilimentum-decorated webs were built interspersed with undecorated webs. *Cyclosa conica* might have recycled their orb each day because the web diameters as well as number and location of wrapped prey recorded from the same web site varied from day to day. *Cyclosa conica* have also been reported to incorporate wrapped prey into stabilimenta (Marples 1969; Levi 1977); but those in my study frequently left the wrapped prey where the insects were intercepted on the web. The recorded position and number of wrapped prey on webs indicated that spiders seldom retain wrapped prey and stabilimenta. Among the 24 decorated webs recorded, only four of them contained wrapped prey in the stabilimenta.

Tests.—This study was conducted in June and July, 1992, at the University of Michigan Biological Station near Pellston, Michigan. I tested insect-attraction as one of the functions of stabilimenta spun by *C. conica* by comparing the daily insect interception rates (DIIRs) between stabilimentum-decorated and undec-orated webs. However, in addition to stabilimenta, the size and the location of a web may also affect its DIIR. Previous studies suggested that larger webs may potentially trap more insects than smaller webs (Brown 1981; Craig 1989; Higgins & Buskirk 1992). Because of the heterogeneous distribution of insects, the location of a web may also greatly affect its insect trapping ability (Craig 1989). Therefore, I tested the insect-attraction hypothesis by comparing (1) the DIIRs between stabilimentum-decorated and undecorated webs, (2) the difference in web diameter between decorated and undecorated webs, and (3) DIIRs of the same type of web (decorated or undecorated) collected from different web locations. The insect-attraction hypothesis can be supported if (1) the decorated webs intercepted more insects, (2) the decorated webs were no larger webs than undecorated webs, and (3) the average insect trapping rates of the same type of webs did not differ between various web locations.

Census methods.—Web locations of *C. conica* were marked by fastening green tape on the tree trunk a meter below the web. Webs from all locations ($n = 13$) were monitored each day between 0800–1800 h. The number of days those web locations remained occupied ranged from 5–13 days. Web diameter (cm) and presence of stabilimenta were recorded once at 0800 h. The number of wrapped prey per web per 10 hours of observation (between 0800–1800) was used as an estimate of DIIR, and the webs were monitored three times a day. I also mapped the position of wrapped prey on webs to check if the spiders reused the old web, thus recounting of the previously wrapped prey was avoided. In most cases there was no wrapped prey on webs at the time of web diameter measurement. A total of 93 DIIRs was collected, among them 24 were from decorated webs (from seven locations; webs from six other locations were all undecorated) and 69 were from undecorated webs (from all 13 locations).

Statistical analysis.—To examine the effect of stabilimenta, I used a Mann-Whitney *U*-test to compare the DIIRs collected from decorated and undecorated webs. I also used a Mann-Whitney *U*-test to compare the web diameters between two types of webs. Kruskal-Wallis one way ANOVAs were used to
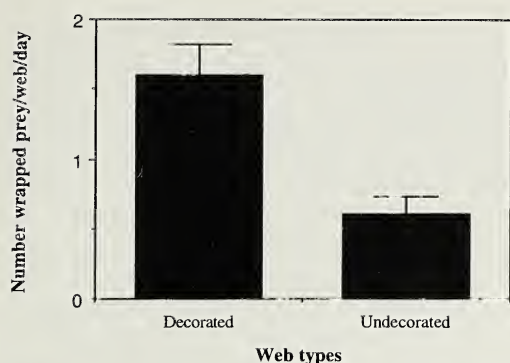
Figure 1.—Means (± SE) of daily insect interception rates (number of wrapped prey per web per 10 hours of observation) of the stabilimentum-decorated and undecorated webs spun by *Cyclosa conica* (Pallas).
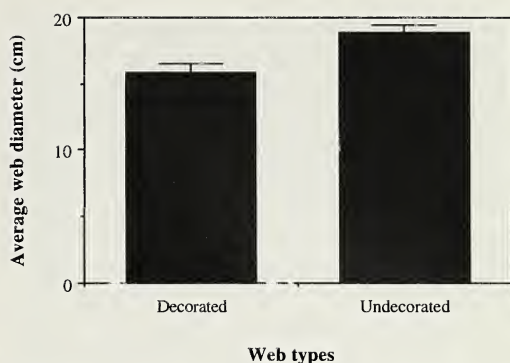

Figure 2.—Means (± SE) of web diameters (cm) of the stabilimentum-decorated and undecorated webs spun by *Cyclosa conica* (Pallas).

determine if differences existed between (1) DIIRs of decorated webs collected from seven locations and (2) DIIRs of undecorated webs collected from 13 locations. In both ANOVA analyses, web locations were used as categories to sort DIIRs collected. By performing two Kruskal-Wallis ANOVAs on DIIRs collected from two types of webs, the effect of web location on insect interception can be separated from the effect of the stabilimenta, since only one category was used in each ANOVA analysis.

RESULTS

Decorated webs spun by *Cyclosa conica* intercepted significantly more prey than undecorated webs (Mann-Whitney U statistic = 389.0, $P = 0.000$, Fig. 1). Although decorated webs contained almost 150% more wrapped prey than undecorated webs, their web diameters were significantly smaller by 18.9% (Mann-Whitney U statistic = 1156.0, $P = 0.004$, Fig. 2). Although the web location was known to affect its trapping efficiency, decorated as well as undecorated webs at different locations trapped similar numbers of insects. There was no difference in DIIRs of decorated webs collected from seven web locations (Kruskal-Wallis statistic = 9.363, $df = 6$, $P = 0.154$), nor was there difference in DIIRs of undecorated webs collected from 13 web locations (Kruskal-Wallis statistic = 7.727, $df = 12$, $P = 0.806$). These results suggested that the difference in the number of wrapped prey between decorated and undecorated webs re-

sulted from the presence of stabilimenta, rather than from the difference in web diameters or the differential distribution of insects among web locations.

DISCUSSION

The hypothesis that presence of stabilimenta increased insect interception of webs spun by *Cyclosa conica* was supported by the results. Decorated webs intercepted almost 150% more insects than did undecorated webs. The higher DIIR of decorated webs seemed to result from presence of stabilimenta, instead of from size variation between two types of webs or from differential insect distribution between web locations. Moreover, the average web diameter of decorated webs was significantly smaller than that of undecorated webs, and prey interception did not differ between different web locations. Compared to similar studies on other stabilimentum-building taxa such as *Argiope argentata* (31.3%, Craig & Bernard 1990) and *Argiope trifasciata* (72% more flying insects, Tso 1996), this gain in insect interception is exceedingly high.

The higher trapping efficiency and the smaller diameter of decorated webs spun by *Cyclosa conica* provides an important insight to the foraging ecology of this orb-weaving spider. The size of an orb web, in addition to other web characteristics, is known to affect its insect trapping efficiency. Studies on several orb-weaving spiders demonstrated that larger webs tended to trap more prey (Brown 1981; Craig 1989; Higgins & Buskirk 1992). Recent studies further demonstrated that some orb-weaving spiders may manipulate their orb

size when prey intake varies. Sherman (1994) reported that *Larinioides cornutus* (Clerck 1757), while maintaining same mesh size, decreased web diameters after food-satiation and increased web diameter when experiencing a long period of hunger. Higgins & Buskirk (1992) demonstrated that *Nephila clavipes* (Linnaeus 1767) built larger webs in habitats of lower prey abundance. Although some of the studies did not consider the potential effect of other web characteristics, they did indicate that orb size must be considered when evaluating the prey interception of orb-webs. However, in this study the average web diameter of decorated webs was almost 20% smaller than that of undecorated webs, but the average prey interception rate was 150% more. This result suggested that in the future study of foraging ecology using orb-weaving spiders, in addition to the commonly known web characteristics such as orb size, mesh size and web location, silk stabilimenta (if exhibited by the taxa studied) should also be included in the analysis.

The effectiveness of stabilimenta built by *Cyclosa conica* in attracting prey greatly exceeds that of *Argiope* spiders investigated so far, which may result from the different types of habitats occupied by the spiders. *Cyclosa conica* typically build their webs in the differentially shaded forest understory in which the light intensity is dim (Marples & Marples 1937; Levi 1977). In contrast, *Argiope* spiders tend to choose an open field—a very bright light environment—as web sites (Levi 1968). The insects available to *C. conica* are mostly small dipterans and hymenopterans (collected from sticky traps, Tso unpubl. data), characterized by high flight maneuverability and the capability of detecting and avoiding spider webs (Craig 1986). However, those insects respond quite differently to spider webs hanging in different light environments. Webs in the dim forest understory are less visible to those insects, making the webs more difficult to avoid than those in the bright open field (Craig 1988). The dim light environment, plus the extremely fine silk characteristic of *C. conica* (Comstock 1913; Marples & Marples 1937), may make the webs difficult to detect by those insects (Craig 1986). Although the decorated webs of both *Argiope* and *Cyclosa* spiders can attract insects to orient toward them, the lower web visibility of the latter

may allow approaching insects less time to avoid the web, therefore leading to higher insect interception.

The results from this study suggest that the presence of stabilimenta can potentially increase the foraging efficiency of *Cyclosa conica*. However, one important question still remains unanswered. That is, given the gain in prey intake generated by stabilimenta, why do *C. conica* and *Argiope* spiders not always build stabilimenta on their webs? The study by Craig (1994) on *Argiope argentata* provided an evolutionary solution to the riddle of inconsistency in stabilimentum-building. Craig (1994) demonstrated that the highly unpredictable pattern and building frequency of stabilimenta could prevent hymenopteran insects from learning from past experience to associate stabilimenta with danger. Craig (1994) suggested that a consistent building of stabilimenta (in both shape and frequency) was disadvantageous to *Argiope* spiders because some insects could learn from past experience to associate stabilimenta with danger and would actively avoid decorated webs in future encounters. Craig (1994) thus provides a possible evolutionary explanation (an ultimate factor) for the inconsistency in stabilimentum-building. However, although Eberhard (1973) and Lubin (1986) provided evidence that light intensity may affect stabilimentum-building of nocturnal uloborids, how stabilimentum-building is proximately controlled in diurnal orb weavers is not clear. Edmunds (1986) and Nentwig & Rogg (1988) examined the effect of microclimatic conditions, habitat type, web characteristics, presence of males, illumination, prey abundance, ecdysone and even heredity on stabilimentum-building of various *Argiope* spiders. But none of the factors examined could significantly affect the building of silk stabilimenta. Although this study demonstrates that silk stabilimenta may increase spiders' foraging, the lack of knowledge regarding ecological factors controlling the building of stabilimenta (which result in the role stabilimenta play in the ecology of spiders unclear) greatly reduces the validity of prey-attraction hypothesis. Therefore, the identification of proximate factors controlling stabilimentum-building is essential to fully realize how silk stabilimenta is involved in the ecology of more than 17 genera of orb-weaving spiders.

LITERATURE CITED

Brown, K.M. 1981. Foraging ecology and niche partitioning in orb-weaving spiders. Oecologia, 50: 380–385.

Chacon, P. & Eberhard, W.G. 1980. Factors affecting numbers and kinds of prey caught in artificial spider webs, with consideration of how orb webs trap prey. Bull. British Arachnol. Soc., 5:29–38.

Comstock, J.H. 1913. The Spider Book. Doubleday, Page & Company, Garden city, New York.

Craig, C.L. 1986. Orb-web visibility: the influence of insect flight behavior and visual physiology on the evolution of web designs within the Araneoidea. Anim. Behav., 34:54–86.

Craig, C.L. 1988. Insect perception of spider orb webs in three light habitats. Funct. Ecol., 2:277–282.

Craig, C.L. 1989. Alternative foraging modes of orb web weaving spiders. Biotropica, 21:257–264.

Craig, C.L. & G.D. Bernard. 1990. Insect attraction to ultraviolet-reflecting spider webs and web decorations. Ecology, 71:616–623.

Craig, C.L. 1991. Physical constraints on group foraging and social evolution: observations on web-spinning spiders. Funct. Ecol., 5:649–654.

Craig, C.L. 1994. Predator foraging behavior in response to perception and learning by its prey: interactions between orb-spinning spiders and stingless bees. Behav. Ecol. Sociobol., 35:45–42.

Eberhard, W.G. 1973. Stabilimenta on the webs of *Uloborus diversus* (Araneae: Uloboridae) and other spiders. J. Zool., London, 171:367–384.

Eberhard, W.G. 1986. Effects of orb-web geometry on prey interception and retention. Pp. 70–100, *In* Spiders, Webs, Behavior and Evolution. (W. Shear, ed.). Stanford Univ. Press.

Eberhard, W.G. 1990. Function and phylogeny of spider webs. Ann. Rev. Ecol. Syst., 21:341–372.

Edmunds, J. 1986. The stabilimenta of *Argiope flavipalpis* and *Argiope trifasciata* in west Africa, with a discussion of the function of stabilimenta. Pp. 61–72, *In* Proc. of the Ninth Intern. Congr. Arachnol., Panama, 1983, Smithsonian Instit. Press. Washington, D.C.

Higgins, L.E. & R.E. Buskirk. 1992. A trap-building predator exhibits different tactics for different aspects of foraging behavior. Anim. Behav., 44:485–499.

Kerr, A.M. 1993. Low frequency of stabilimenta in orb webs of *Argiope appensa* (Araneae: Araneidae) from Guam: an indirect effect of introduced avian predator? Pacific Sci., 47:328–337.

Kaston, B.J. 1948. Spiders of Connecticut. Connecicut Geol. Nat. Hist. Surv., Bulletin No. 70.

Levi, H.W. 1968. The spider genera *Gea* and *Argiope* in America (Araneae: Araneidae). Bull. Mus. Comp. Zool., 136:319–352.

Levi, H.W. 1977. The American orb-weaver genera, *Cyclosa, Metazygia* and *Eustala* north of Mexico (Araneae, Araneidae). Bull. Mus. Comp. Zool., 148:247–338.

Levi, H.W. 1983. The spider genera, *Argiope, Gea*, and *Neogea* from the west region (Araneae: Araneidae, Argiopinae). Bull. Mus. Comp. Zool., 150:247–38.

Lubin, Y.D. 1986. Web building and prey capture in Uloboridae. Pp. 132–171, *In* Spiders, Webs, Behavior and Evolution. (W. Shear, ed.). Stanford Univ. Press.

Marples, J. & B.J. Marples. 1937. Notes on the spiders *Hytiotes paradoxus* and *Cyclosa conica*. Proc. Zool. Soc. London, CVII (A):213–221.

Marples, B.J. 1969. Observations on decorated webs. Bull. British. Arachnol. Soc, 1:13–18.

Nentwig, W. & S. Heimer. 1987. Ecological aspects of spider webs. Pp. 216–221, *In* Ecophysiology of Spiders. (W. Nentwig, ed.),Springer-Verlag. Berlin.

Nentwig, W. & H. Rogg. 1988. The cross stabilimentum of *Argiope argentata* (Araneae: Araneidae) – nonfunctional or a nonspecific stress reaction. Zool. Anz., 221:248–266.

Robinson, M.H. & B. Robinson. 1970. The stabilimentum of the orb web spider *Argiope argentata*: an improbable defense against predators. Canadian Entomol., 102:641–655.

Rovner, J.S. 1976. Detritus stabilimenta on the webs of *Cyclosa turbinata* (Araneae, Araneidae). J. Arachnol., 4:215–16.

Schoener, T.W. & D.A. Spiller. 1992. Stabilimenta characteristics of the spider *Argiope argentata* on small islands: support for the predator-defense hypothesis. Behav. Ecol. Sociobiol., 31:309–318.

Sherman, P.M. 1994. The orb-web: an energetic and behavioral estimator of a spider's dynamic foraging and reproductive strategies. Anim. Behav., 48:19–34.

Tso, I.M. 1996. Stabilimentum of the garden spider *Argiope trifasciata*: a possible prey attractant. Anim. Behav., 52:183–191.

Yaginuma, T. 1986. Spiders of Japan in color. Osaka, Hikusha Publishing Co., Ltd.

COPULATORY PATTERN AND FERTILIZATION SUCCESS IN MALE WOLF SPIDERS WITHOUT PRE- OR POST-COPULATORY SPERM INDUCTION

Fernando G. Costa: Etología, División Zoología Experimental, Instituto de Investigaciones Biológicas Clemente Estable, Av. Italia 3318, Montevideo, Uruguay

ABSTRACT. Experiments with *Lycosa malitiosa* Tullgren 1905 were carried out to determine: a) whether males that had never performed sperm induction can copulate, b) whether these males perform an altered copulatory pattern, and c) whether the stored sperm from a single sperm induction is enough to inseminate two consecutive females. A group of males whose genital pores were sealed with melted paraffin immediately after molting copulated once; then, the seal was removed, and later these males copulated again. A second group of males was untreated prior to their first copulation but then immediately had their genital pores sealed and subsequently were allowed to copulate again. Two other groups of males were used as controls: their genital pores were "pseudosealed" by having paraffin placed beside them. All females were virgins, and the number of progeny produced by each was recorded. Males that never had sperm in their palps maintained the basic species-specific copulatory pattern, although they showed several minor copulatory alterations. The second copulation of males prevented from recharging their palps resulted in the production of abundant progeny. Matings of older males (second copulations) resulted in a similar number of spiderlings as that of younger males (first copulations).

Since Petrunkevitch (1911) some authors have assumed that the presence of sperm filling the palpal duct would be indispensable for male spiders to initiate sexual activities (see review in Rovner 1966). More than 50 years later Rovner (1966) experimentally demonstrated that this assumption was not true for the lycosid *Rabidosa rabida* (Walckenaer 1837). This author observed courtship in males where sperm induction was prevented by several methods: induced palpal autotomy, sealing genital pore, sealing spinnerets, or fixing the palps on the cephalothorax. Those earlier assumptions were probably based on observations of recently molted males, during the short period in which males do not court. Male spiders usually perform an initial sperm induction before copulation, although some linyphiids do it only after completing a series of insertions early in copulation (Rovner 1967).

The aim of this study was to test if copulation takes place using males with "empty" palps and, if it occurs, whether the copulatory pattern is altered. Also, the study examines if the amount of sperm originally stored in the palps is sufficient to assure the success of a second copulation (i.e., when sperm induction is prevented following the first copulation).

Experiments were carried out using individuals of *Lycosa malitiosa* Tullgren 1905, a common large-sized wolf spider from southern Uruguay. Its sexual behavior, brood size and reproductive strategy, as well as its phenology, are well known (Costa 1975, 1979, 1991; Costa & Capocasale 1984, 1985; Capocasale et al. 1984).

METHODS

Subadults of *Lycosa malitiosa* were collected in Marindia, Canelones, Uruguay, during Fall 1987 and raised to adults in the laboratory. Forty-eight adult males and 83 adult females were used. Spiders were kept in individual cages and mainly fed with *Tenebrio* sp. larvae (Coleoptera). For other rearing details see Costa (1979) and Costa & Capocasale (1984). For male-female encounters, males were introduced in a wide arena (cylindrical cage of 18 cm diameter), where the female had been placed one or more days before.

Adult males were assigned to four groups (I, II, III and IV). Males observed during molting process were randomly placed in groups I or III; the other males were randomly placed in groups II or IV. Each group was initially composed of 12 males. Every male was involved in two experimental phases: Phase

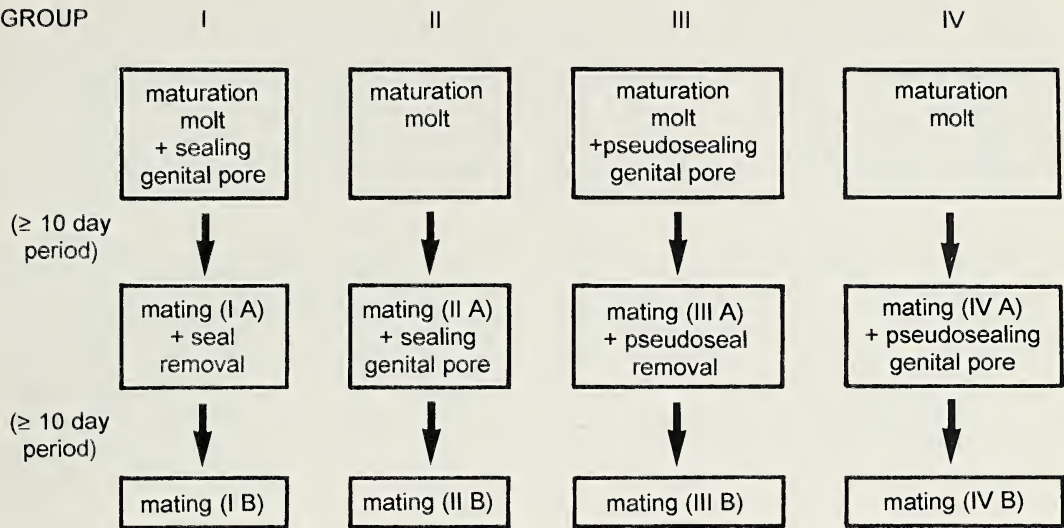| GROUP	I	II	III	IV

Figure 1.—Diagrammatic representation of the experimental design involving male *Lycosa malitiosa*. Males of each group copulated first (subgroup A) ten or more days after the final molt, and copulated again (subgroup B) ten or more days after their first copulation.

A, when males mated for the first time, and Phase B, when males copulated again. Thus, a total of eight copulation subgroups were established: IA, IB, IIA, IIB, IIIA, IIIB, IVA and IVB (Fig. 1). All females used were virgins.

Group I.—Subadult males were monitored as long as possible to observe their maturation molt. When ecdysis was completed, the spider was observed for one hour to permit the hardening of the new cuticle and to ensure that sperm induction did not occur. Males were anaesthetized with CO_2 and their genital pores were sealed using melted paraffin. Ten or more days after molting, males engaged in their first copulation (subgroup IA). Immediately after copulation, these males were anaesthetized with CO_2 and the seal was removed. Ten or more days after their first mating these males mated again with other virgin females (subgroup IB).

Group II.—In subgroup IIA, males copulated 10 or more days after their maturation molt; immediately after copulation, males were anaesthetized and their genital pores were sealed. Ten or more days later, they had a second copulation with a virgin female (subgroup IIB).

Group III.—Subadult males were watched until their maturation molt. Newly-emerged males were observed for one hour to ensure against sperm induction. Then they were an-

aesthetized and melted paraffin was placed beside the genital pore ("pseudoseal"), avoiding sealing it. Ten or more days after pseudosealing, males of this IIIA subgroup copulated with virgin females. They were immediately anaesthetized and the pseudoseal was removed. Ten or more days after the first mating, these males (subgroup IIIB) remated with virgin females.

Group IV.—Males copulated 10 or more days after their maturation molt (subgroup IVA) and immediately were anaesthetized and pseudosealed. Ten or more days after their first copulation, these males (subgroup IVB) recopulated with virgin females.

A schematic representation of the palpal condition of the eight experimental subgroups is given in Table 1. One male from group I died of natural causes before his first copulation. Second copulations were less numerous than were first copulations: they diminished by three in group I, three in group II, four in group III and one in group IV. This diminution was caused by unsuccessful courtship (three cases), male deaths due to natural causes (four cases), female bite (three cases), and accidental damage during manipulation (one case).

The course of copulatory behavior was recorded on forms that organized data on general copulatory pattern, alternation in the use of the palps, and number and duration of pal-

Table 1.—Male palpal condition before mating in the experimental groups. For experimental design see Figure 1.

Male group	I	II	III	IV
Phase A	without sperm	with sperm	control (with sperm)	with sperm
Phase B	with sperm	sperm not replaced	with sperm	contral (with sperm)

pal insertions. As described by Costa (1979) and Costa & Sotelo (1994), two main copulatory phases occur in *L. malitiosa*: Pattern I (PI) consists of multiple consecutive insertions with the same palp, change of side, multiple insertions with the other palp, and so on. Pattern II (PII) follows PI and consists of alternate use of the palps after a single insertion. "Brief" insertions consisted of the palp engaging in the epigynum, complete hematodochal distension with simultaneous spine erection, then immediate disengagement, collapse of the hematodocha, and rapid spine descent. I considered as "many" brief insertions the occurrence of more than 20 in a copulation; and "few", between 5–20 in a copulation (less than five was not considered). Pseudoinsertions, if the palp disengaged from the female epigynum before complete swelling of the hematodocha and/or complete spine erection, were not counted as insertions.

Males were sacrificed immediately after their second copulation, using carbon tetrachloride vapors. Mated females were maintained in the laboratory. The numbers of both egg sacs and spiderlings were recorded. Juveniles were removed from the female's back after 10 days following their emergence, a time when they disperse in nature. One female from subgroup IVA died before completing reproduction and was not considered. Male and female voucher specimens were deposited in the arachnological collection of the Museo Nacional de Historia Natural, Montevideo.

In the analysis, groups I and II were compared with their respective controls, III and IV, always within the same experimental phase (A or B). In some cases both phases were compared between them within the same group. Both two-tailed statistics Student *t*-test and Mann-Whitney U-test were used.

RESULTS

Copulatory characteristics of the experimental groups are given in Table 2. Copulation durations were similar among the groups.

Only durations from subgroup IVA showed low values, particularly in comparison with subgroups IIA and IVB, but did not show significant differences using the Student *t*-test. Differences in copulation duration among the subgroups were not correlated with environmental temperature variations. The two shortest copulations correspond to low temperatures.

The species-specific pattern of copulation was basically maintained in all experimental groups. The number of total insertions did not show significant differences among groups using the U-test. However, the values from subgroup IA and especially subgroup IB were the highest. No differences among subgroups were found when comparing separately Pattern I or Pattern II. However, insertions were very numerous in both the PI and PII copulatory patterns of subgroup IB.

Modifications were numerous in subgroups IA and IB, while they were minimal in IIA. The more frequent modifications of the copulatory pattern were: (1) occurrence of "few" and "many" brief insertions (see Methods); (2) occurrence of pseudoinsertions; (3) Pattern II very short or absent; and (4) occurrence of some multiple consecutive insertions of the same palp intercalating Pattern II (Table 2). Modifications were numerous in subgroups IA and IB, while they were minimal in IIA.

The number of progeny produced by females is shown in Fig. 2. Considering the mean total number of spiderlings, high values were observed in subgroups IIA, IIIA, and IVB. Total juvenile number from IIA did not show a significant difference when compared with IVA ($U = 34$), although P was near the 0.05 level. No offspring were produced by females of subgroup IA. A low number of spiderlings was found in IB, reflecting the absence of progeny in four of the nine females. These values were just significant in relation to the IIIB values ($U = 15$; $P = 0.05$). Low progeny values of females of subgroup IVA
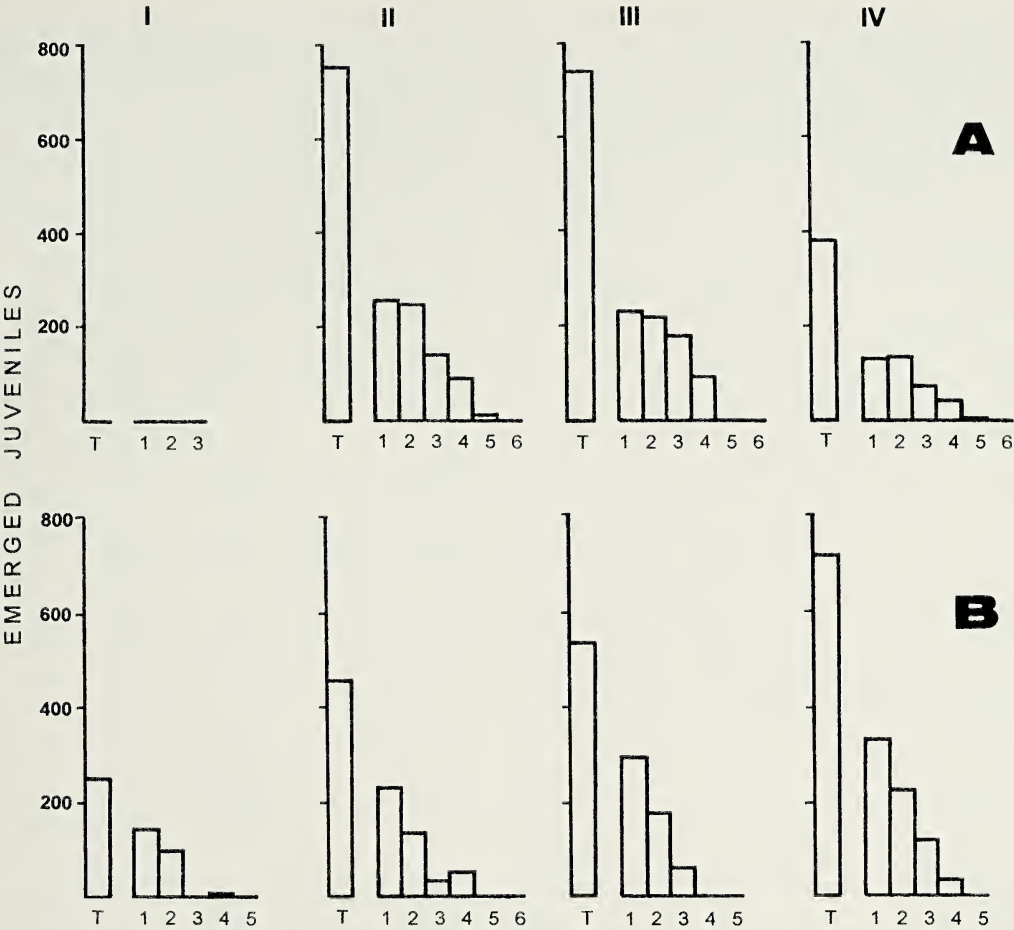
Figure 2.—Progeny from the four experimental female groups. Bars indicate mean values of spiderlings: total values (T) and number of spiderlings emerged from each egg sac (first = 1, second = 2, etc.). Zero values were included. Clutch numbers without bars indicate occurrence of egg sacs but no juveniles. For details of experimental design, see Figure 1.

also resulted in significant differences compared to subgroup IVB ($U = 25.5$; $P < 0.05$).

As to the copulatory pattern, the number of alterations in palpal insertions for each experimental subgroup (Table 2) showed an inverse correlation with the number of progeny produced ($r = -0.809$, $P < 0.05$). No differences among groups were found in either male or female age during copulation (Table 3). No differences in the number of progeny were found when comparing Phase A with Phase B within the same group, with the exception of IA vs. IB subgroups. (As a result of the experimental plan, males mating in Phase B were older than males mating in Phase A.)

The number of egg sacs varied between 4–6, except subgroup IA in which there was a mean of three egg sacs. The subgroup IA egg sacs were immediately eaten or abandoned.

All males, excepting the sealed IIB males, had a whitish drop in the genital pore region when examined after they were sacrificed.

DISCUSSION

Results show that male *Lycosa malitiosa* maintain full sexual activity despite the absence of sperm in their palps. These results agree with the observations of Rovner (1966, 1967) in lycosid and linyphiid spiders. Although the male copulatory behavior of subgroup IA followed the normal species-specific pattern (Costa 1979; Costa & Sotelo 1994), atypical copulations were frequent. Only four matings of 12 were completely typical, which

Table 2.—Summary of copulatory characteristics from experimental groups of *Lycosa malitiosa*. Each male performed two consecutive copulations (A and B), each with two virgin females. Abbreviations: Number of observed matings (# obs.); copulation duration (CD); copulatory patterns I and II (PI and PII); main copulatory alterations number: Brief insertions (BI: several and few), pseudoinsertions (pseudoins.), reduced pattern II (PII brief), and multiple insertions during pattern II (PII-MI).

Subgroup	IA	IB	IIA	IIB	IIIA	IIIB	IVA	IVB
# obs.	12	9	12	9	12	8	11	10
CD (min)								
Mean	68.7	76.7	75.6	72.7	76.7	79.1	59.1	77.8
SD	25.8	30.8	17.7	15.9	21.5	27.5	25.3	16.8
Temp. (°C)								
Mean	24.5	25.8	25.0	26.5	25.0	26.3	25.0	25.7
SD	2.3	2.8	3.0	2.1	2.3	2.3	2.7	2.4
Palpal insertions (Total)								
Mean	314.4	376.3	273.3	291.6	268.0	254.4	238.6	267.7
SD	82.3	174.8	53.8	77.9	75.7	120.8	95.8	94.5
PI								
Mean	271.8	309.8	225.6	244.6	215.5	207.6	196.5	221.7
SD	62.9	147.9	51.2	75.8	67.4	107.7	80.4	83.1
PII								
Mean	42.7	66.6	47.8	47.0	52.5	46.9	42.1	46.0
SD	24.5	43.1	15.8	22.2	13.7	16.0	27.8	21.9
Alterations in palpal insertions								
BI/Several	4	3	0	3	2	1	1	2
BI/Few	5	3	1	1	1	2	3	3
Pseudoins.	2	2	0	0	2	0	2	2
PII brief	3	1	0	1	0	0	3	1
PII-MI	5	4	1	4	3	2	1	3
Progeny								
Mean	0	249.0	753.8	453.0	737.8	529.5	381.7	716.1
SD	—	294.1	498.6	244.5	366.0	296.8	283.7	374.7
Females without progeny	12	4	0	1	0	0	2	0

Table 3.—Adult age (days post-final molt) of copulating males (M) and females (F) in the experimental groups of *Lycosa malitiosa*. *n* = number of copulations per group.

	Group							
	I		II		III		IV	
	M	F	M	F	M	F	M	F
Phase A								
Mean	39.1	13.9	40.4	21.3	41.4	15.0	40.8	28.1
SD	17.9	7.7	19.2	23.4	15.1	10.0	17.4	24.0
n	12		12		12		11	
Phase B								
Mean	79.4	10.7	91.3	15.4	85.3	10.4	83.5	22.2
SD	35.5	6.4	37.5	9.6	24.1	8.2	36.9	22.0
n	9		9		8		10	

might be attributed to the particular experimental procedure. However, other factors probably are involved, considering that males with sperm in their palps also showed atypical behaviors. The lack of progeny from IA females confirmed that sealing the male gonopore prevented sperm uptake by the palps completely. It also indicated that parthenogenesis does not occur in the studied population of *L. malitiosa*, as was suggested in the dysderid *Dysdera hungarica* Kulczynski 1897 (Deeleman-Reinhold 1986). Females of subgroup IA made unsuccessful egg sacs, as described also by Capocasale et al. (1984) for virgin females of this species.

Maintenance of the typical species-specific copulatory pattern in subgroup IA indicated that copulation is mainly performed independently of proprioceptive information generated by the presence of sperm in the palpal duct. Seminal fluid released into the palpal duct could substitute for the sperm and help to maintain the typical copulatory mechanics; however, copulatory maneuvers probably are determined primarily by neural centers. Rovner (1967) observed "pseudocopulations" similar to normal copulations in palpectomized males of *Linyphia triangularis* (Clerck 1757) (Linyphiidae).

Copulation duration did not show significant variations among experimental subgroups, including subgroup IA. Copulation duration in subgroup IVA was brief. This group also showed many alterations in the copulatory pattern and small number of progeny from females. Considering that the same males showed normal copulation and progeny in IVB, the result in IVA was surprising and could be attributed to chance.

The well-established relationship between copulation duration and environmental temperature in this species (Costa 1979; Costa & Sotelo 1984, 1994) did not determine the differences observed here in copulatory duration. Shortest copulations of subgroups IA and IVA disagree with the inverse relationship noted by these authors.

The fact that the greatest number of palpal insertions was performed by subgroup IB suggested some unknown influence of the application and removal of the genital pore seal. This subgroup showed a typical copulation duration, which may be explained by the short duration of many of these insertions (several

"brief" insertions). The small number of progeny produced by IB females could be attributed to the occurrence of brief insertions and other copulatory alterations (see Table 2). However, subgroup IVB, which presented an occurrence of copulatory alterations similar to IB, generated abundant progeny. It is most likely that the seal removal procedure used in group I was imperfect, interfering with sperm induction in some males. The probability of incomplete seal removal was supported by the absence of offspring in four IB females, and a relatively small number of progeny (448.2 ± 247.8 spiderlings) in the other five females.

Subgroup IIB produced a moderate number of progeny. Males from this group had been prevented from recharging their palps after their first copulation (postcopulatory sealing of the genital pore). Their first copulation was normal and generated abundant progeny. Despite this "emptying", the "residual" sperm were sufficient in number to yield a relatively high number of spiderlings in IIB, especially considering that it involved a number of copulatory modifications. The sperm storage capacity of *L. malitiosa* males is large; and sperm remains viable during the long period of consecutive ovipositions, between 6–7 months in warm conditions (Costa & Capocasale 1985; Costa 1991). The abundance of sperm is confirmed by one particular observation: one male from subgroup IVA failed to insert its left palp during an entire mating that yielded 530 spiderlings. In *L. malitiosa*, the occurrence of multiple copulations in the females (Costa 1979) would primarily have advantages other than renewing the sperm supply (see review from Austad 1984).

The sperm droplet that was exuded onto the surface surrounding the male's genital pore after mating was not observed in other males which had not recently copulated and which had been similarly sacrificed. Perhaps sperm accumulates at the end of the male's genital duct stimulated by copulation, "waiting for" an immediate postcopulatory sperm induction.

Abundant progeny resulted from subgroups IIA, IIIA and IVB in numbers similar to those obtained by Capocasale et al. (1984) for female *L. malitiosa* reared under similar conditions. The other subgroups showed reductions, suggesting some influence of the experimental procedure. However other factors, such as cryptic female choice during copulation

(Eberhard 1994), could be acting and affecting each experimental subgroup differently.

Experimental groups III and IV were the controls for groups I and II; they provided tests for the effects of experimental manipulations (anaesthesia and paraffin application) on spider performance. Results from IIIA and IVB indicate that experimental manipulations did not affect either the copulatory characteristics or the number of progeny produced by the spiders. The unexpected copulatory modifications and low production of progeny occurring in IVA, cannot be explained. These males had filled their palps before copulation and followed an experimental procedure similar to subgroup IIA; also, they were the same individuals subsequently used for subgroup IVB, which had a normal number of progeny.

Female age was similar among subgroups, but the used method involved two different age classes of males, according their use in first or second matings. The average age of males during second copulations ranged between 80–90 days post-final molt, which was close to the age they normally died under laboratory conditions (101.3 ± 21.1 days post-final molt; Costa 1985). Male senility during attempted second copulations probably caused some of the female rejections observed during courtship. However, no significant differences were found in copulatory duration or pattern, nor between the number of progeny produced by first or second matings (group I was obviously excluded). The results for copulation duration in *L. malitiosa* do not agree with the positive correlation between both female and male age and copulation duration reported for the lycosid *Schizocosa ocreata* (Hentz 1844) (see Hebets & Uetz 1995).

ACKNOWLEDGMENTS

LITERATURE CITED

Austad, S.N. 1984. Evolution of sperm priority patterns in spiders. Pp. 223–249, *In* Sperm competition and the evolution of animal mating systems. (R.L. Smith, ed.). Academic Press, Orlando, Florida.

Capocasale, R.M., F.G. Costa & J.C. Moreno. 1984. La producción de ootecas de *Lycosa malitiosa* Tullgren (Araneae, Lycosidae). II, Análisis cuantitativo de hembras vírgenes y copuladas. Aracnología, 3:1–7.

Costa, F.G. 1975. El comportamiento precopulatorio de *Lycosa malitiosa* Tullgren (Araneae, Lycosidae). Rev. Brasileira Biol., 35:359–368.

Costa, F.G. 1979. Análisis de la cópula y de la actividad postcopulatoria de *Lycosa malitiosa* Tullgren (Araneae, Lycosidae). Rev. Brasileira Biol., 39:361–376.

Costa, F.G. 1985. El desarrollo de los estadios juveniles de *Lycosa malitiosa* en condiciones de laboratorio (Araneae, Lycosidae). Actas Jornadas Zool. Uruguay: 66–68.

Costa, F.G. 1991. Fenología de *Lycosa malitiosa* Tullgren (Araneae, Lycosidae) como componente del criptozoos en Marindia, localidad costera del sur del Uruguay. Bol. Soc. Zool. Uruguay, 2a. época, 6:8–21.

Costa, F.G. & R.M. Capocasale. 1984. La producción de ootecas de *Lycosa malitiosa* Tullgren (Araneae, Lycosidae). I, Importancia de la muda de maduración sobre la primera oviposición. Aracnología, 2:1–8.

Costa, F.G. & R.M. Capocasale. 1985. La producción de ootecas de *Lycosa malitiosa* Tullgren (Araneae, Lycosidae). III, Distribución de las oviposiciones en el tiempo. Aracnología, 5:1–14.

Costa, F.G. & J.R. Sotelo. 1984. Influence of temperature on the copulation duration of *Lycosa malitiosa* Tullgren (Araneae, Lycosidae). J. Arachnol., 12:273–277.

Costa, F.G. & J.R. Sotelo. 1994. Stereotypy and versatility of the copulatory pattern of *Lycosa malitiosa* (Araneae, Lycosidae) at cool *versus* warm temperatures. J. Arachnol., 22:200–204.

Deeleman-Reinhold, C.L. 1986. *Dysdera hungarica* Kulczynski - a case of parthenogenesis? Actas X Congr. Int. Aracnol. Jaca/España, I:25–31.

Eberhard, W.G. 1994. Evidence for widespread courtship during copulation in 131 species of insects and spiders, and implications for cryptic female choice. Evolution, 48:711–733.

Hebets, E.A. & G.W. Uetz. 1995. Copulation duration as a function of male and female age in the wolf spider *Schizocosa ocreata*. American Arachnol., 52:9 (abstract).

Petrunkevitch, A. 1911. Sense of sight, courtship and mating in *Dugesiella hentzi* (Girard), a theraphosid spider from Texas. Zool Jb., Abt. System., Ökol. u Geogr., 31:355–376.

Rovner, J.S. 1966. Courtship in spiders without prior sperm induction. Science, 152:543–544.

Rovner, J.S. 1967. Copulation and sperm induction by normal and palpless male linyphiid spiders. Science, 157:835.

RESEARCH NOTE

THE EFFECTS OF REPRODUCTIVE STATUS ON SPRINT SPEED IN THE SOLIFUGE, *EREMOBATES MARATHONI* (SOLIFUGAE, EREMOBATIDAE)

Costs associated with reproduction are delineated by trade-offs between the current reproductive capacity of an animal and the probability of its future survival and reproductive success (Williams 1966). The successful analysis of life history parameters depends on our ability to identify proximate mechanisms by which such costs are mediated. Documented costs associated with reproduction include decreased survivorship resulting from physiological or behavioral changes that accompany reproduction (Hirshfield & Tinkle 1975; Bell 1980). For example, if escape from a predator depends on the speed or endurance of a potential prey organism, then any reduction in the locomotor performance of gravid females could increase the risk of predation. Locomotor performance has been correlated with survivorship in many species of vertebrates (Shine 1980; Punzo 1982; Huey et al. 1984; Svensson 1988; Brodie 1989; Jayne & Bennett 1990; Plummer 1993) but little information exists for arthropods in general (Winfield & Townsend 1983; Crowl & Alexander 1989; Punzo 1989) or for arachnids specifically (Moffett & Doell 1980; Shaffer & Formanowicz 1996).

Solifuges are common representatives of the arachnid fauna in desert regions worldwide (Turner 1916; Muma 1967; Cloudsley-Thompson 1977; Wharton 1987). These predators may forage over a considerable area actively searching for prey (Muma 1966; Wharton 1987; Punzo 1994b, 1995a), and rely on speed to escape from encounters with aggressive conspecifics or potential predators (Cloudsley-Thompson 1977; Wharton 1987; Punzo 1995b, 1997). In the present study, I compared the sprint speeds of gravid and non-gravid females of the solifuge *Eremobates marathoni* Muma 1970. To my knowledge, no previous data on sprint speed or the relationship between sprint speed and reproductive status exist for the Solifugae.

Eremobates marathoni is a common inhabitant of the Big Bend region of Trans Pecos Texas (Punzo 1997), which lies within the northern confines of the Chihuahuan Desert. I collected gravid (G) and nongravid (NG) females by hand at night with the aid of a head lamp as they wandered over the surface of the ground, or through the use of pitfall traps as described previously (Punzo 1994a). All solifuges were collected within a 3 km radius of Marathon, Texas (Brewster County) during July 1996. A detailed description of the geology and dominant vegetation of this area is given by Tinkam (1948).

Solifuges were transported back to the laboratory, housed individually in plastic containers (30 × 15 × 10 cm), and fed on a diet of crickets and mealworm larvae as described by Punzo (1997b). Gravid females were identified by the presence of embryos visible through the ventral body wall. I recorded the following measurements for each G and NG female: body length (BL) in mm; width of propeltidium (WP) in mm, and body weight (BW) in grams. Adult solifuges, as well as eggs, were maintained at 25–27 °C and 70–72% relative humidity in a Percival Model 816 environmental chambers (Boone, Iowa). Adult females were removed from these chambers only when subjected to sprint speed analyses. Voucher specimens have been deposited in the Invertebrate Collection at the University of Tampa.

I measured the sprint speed of 20 solifuges

Table 1.—Measurements for body length (BL) and width of propeltidium (WP) in millimeters, body weight in grams, and sprint speed (cm/sec) for females of *Eremobates marathoni*. Data represent means (±SD) for 20 females for each of the following groups: nongravid females; gravid females while carrying embryos and 24 hours post-oviposition.

	Nongravid	Gravid	Post-oviposition
Body length	23.8 (2.1)	22.7 (1.5)	23.1 (2.7)
Propeltidium width	5.71 (0.4)	6.14 (0.6)	5.84 (0.2)
Body weight	3.49 (0.2)	4.62 (0.1)	3.71 (0.3)
Sprint speed (cm/sec)	23.6 (2.4)	14.5 (1.3)	21.7 (1.9)

in a linear race track (length = 90 cm; width = 6 cm). The floor of the track was constructed of wood and covered with coarse plastic carpet material. The floor was marked at 10 cm intervals with black tape. I attached a piece of clear acrylic tubing (5 cm diameter) that was cut in half lengthwise to the bottom of the floor. This prevented the solifuges from climbing or escaping while running and also eliminated shadows. One end of the track was closed by a plastic panel and designated as the start chamber (10 cm in length) where the solifuge was restrained from entering the runway (80 cm) by a hemispherical cardboard gate positioned between slits in the tube. The plastic panel was fitted with an intake valve through which a gentle stream of compressed air could be introduced in order to initiate running (Punzo 1989). The track was placed under a 50 W fluorescent lamp. Animals were deprived of food for 48 h prior to testing.

Sprint speed trials were conducted on 20 NG females and 20 G females. All of the NG females were tested once. Each of the G females was also tested once at each of two reproductive states: gravid, but prior to oviposition (G), and within 24 h after oviposition (post-oviposition, PO). The amount of time between the initial testing of gravid femles and oviposition ranged from 8–14 days. The first trial for all animals occurred within 4–7 days after being brought to the laboratory. The second trial for PO females occurred two days after oviposition. Each female was weighed immediately following the running trials on a Metler electronic analytical balance and returned to its holding cage.

At the start of each trial, a solifuge was placed in the start chamber with its head facing the runway and allowed to habituate for 2 min prior to running. Following this period, the cardboard gate was lifted manually and a

gentle stream of compressed air was introduced through the intake valve. In response to the air flow, the solifuge would immediately begin to run out of the start chamber and into the runway. Since preliminary observations had indicated that solifuge sprint speed was fastest over the first 40 cm, I used the data for locomotor performance over this distance for all statistical analyses. I used a stopwatch to record the amount of time required for a solifuge to cross the 40 cm mark on the runway. Data on sprint speeds were expressed in cm/sec.

All statistical analyses used in this study follow procedures described by Sokal & Rohlf (1981) and Wilkinson (1984). They were conducted using Stat View (Abacus Concepts, Inc., Berkeley, California) and SYSTAT (SYSTAT, Inc., Evanston, Illinois).

Gravid (G) females ran at a significantly slower speed than nongravid (NG) females (Table 1; $t = 7.14$, $P < 0.01$). Following oviposition, post-oviposition (PO) females ran significantly faster than they did while carrying embryos (Wilcoxon matched pairs test; $z = 3.27$, $P < 0.01$). There was no significant difference between the sprint speeds of NG and PO females.

There were no significant differences in body length (BL) ($t = 0.53$, $P > 0.50$), and width of propeltidium (WP) ($t = 0.65$, $P > 0.35$) between G and NG solifuges used in this study. The mean body weight (BW) of G females was 38.5% higher than that of NG females due to the weight of the embryos and associated body fluids. The number of eggs oviposited per G female ranged from 19–46 with a mean of 26.6 ± 3.8 SD. The number of nymphs per female that successfully completed embryonic development and hatched ranged from 9–32 with a mean of 17.7 ± 2.9 SD.

The results of this study, the first reported for a solifuge, indicate that pregnancy results in a significant reduction in locomotor performance. This has important ecological implications because a decrease in sprint speed may increase the risk of predation in a significant way. Solifuges frequently utilize their locomotor capacities to escape predation. (Predators include scorpions, theraphosid spiders, other solifuges, centipedes, road runners, and badgers (pers. obs.)). Similar results have been reported for the striped scorpion, *Centruroides vittatus* (Say 1887) by Shaffer & Formanowicz (1996). In this study, sprint speed was determined for each female at each of three reproductive states (pregnant, while carrying young on her back, and after neonates had dispersed from her back). Sprint speed for pregnant scorpions averaged 84% of post-dispersal speeds. Sixty five percent of the scorpions carrying young on their backs did not run at all when disturbed and assumed a defensive posture while standing their ground. Sprint speeds for the remaining 35% that did run with young on their backs averaged only 61% of their post-dispersal speeds.

ACKNOWLEDGEMENTS

LITERATURE CITED

Bell, G. 1980. The costs of reproduction and their consequences. American Nat., 116:45–76.

Brodie, E.D. 1989. Behavioral modification as a means of reducing the costs of reproduction. American Nat., 134:225–238.

Cloudsley-Thompson, J.L. 1977. Adaptational biology of Solifugae. Bull. British Arachnol. Soc., 4:61–71.

Crowl, T.A. & J.E. Alexander. 1989. Parental care and foraging ability in male water bugs (*Belastoma flumineum*). Canadian J. Zool., 67:513–515.

Hirshfield, M.F. & D. Tinkle. 1975. Natural selection and the evolution of reproductive effort. Proc. Nat. Acad. Sci., USA, 72:2227–2231.

Huey, R.B., A.F. Bennett, H. John-Alder & K.A. Nagy. 1984. Locomotor capacity and foraging behavior of Kalahari lacertid lizards. Anim. Behav., 32:41–50.

Jayne, B.C. & A.F. Bennett. 1990. Selection on locomotor performance capacity in a natural population of garter snakes. Evolution, 44:1204–1229.

Moffett, S. & G.S. Doell. 1980. Alteration of locomotor behavior in wolf spiders carrying normal and weighted cocoons. J. Exp. Zool., 213:219–226.

Muma, M.H. 1966. Feeding behavior of North American Solpugida. Florida Entomol., 49:199–216.

Muma, M.H. 1967. Basic behavior of North American Solpugida. Florida Entomol., 50:115–123.

Plummer, M.V. 1993. Thermal ecology of arboreal green snakes, *Opheodrys aestivus*. J. Herpetol., 27:254–260.

Punzo, F. 1982. Tail autotomy and running speed in the lizards *Cophosaurus texanus* and *Uma notata*. J. Herpetol., 16:329–331.

Punzo, F. 1989. Effects of hunger on prey capture and ingestion in *Dugesiella echina* Chamberlin (Orthognatha, Theraphosidae). Bull. British Arachnol. Soc., 8:72–79.

Punzo, F. 1994a. Trophic and temporal niche interactions in sympatric populations of *Eremobates palpisetulosus* Fichter and *E. mormonus* (Roewer) (Solpugida: Eremobatidae). Psyche, 101:187–194.

Punzo, F. 1994b. An analysis of feeding and optimal foraging behavior in the solpugid, *Eremobates mormonus* (Roewer) (Solpugida, Eremobatidae). Bull. British Arachnol. Soc., 9:293–298.

Punzo, F. 1995a. Feeding and prey preparation in the solpugid, *Eremorhax magnus* (Solpugida: Eremobatidae). Pan Pacific Entomol., 71:13–17.

Punzo, F. 1995b. Intraspecific variation in life history traits between sympatric populations of *Eremobates palpisetulosus* Fichter and *Eremobates mormonus* (Roewer) (Solpugida, Eremobatidae). Bull. British Arachnol. Soc., 10:109–113.

Punzo, F. 1997. Dispersion, temporal patterns of activity, and the phenology of feeding and mating behavior in *Eremobates palpisetulosus* Fichter (Solifugae, Eremobatidae). Bull. British Arachnol. Soc., 10(8):303–307.

Shaffer, L.R. & D.R. Formanowicz. 1996. A cost of viviparity and parental care in scorpions: Reduced spring speed and behavioral compensation. Anim. Behav., 51:1017–1024.

Shine, R. 1980. "Costs" of reproduction in reptiles. Oecologia, 46:92–100.

Sokal, R.R. & F.J. Rohlf. 1981. Biometry. 2nd ed. W.H. Freeman, San Francisco.

Svensson, I. 1988. Reproduction costs in two sex-role reversed pipefish species (Syngnathidae). J. Anim. Ecol., 57:929–942.

Tinkam, E.R. 1948. Faunistic and ecological studies on the Orthoptera of the Big Bend Region of Trans Pecos Texas. American Midl. Nat., 40: 521–583.

Turner, C.H. 1916. Notes on the feeding behavior and oviposition of a captive American false-spider (*Eremobates fornicaria* Koch). J. Anim. Behav., 6:160–168.

Wharton, R.A. 1987. Biology of the diurnal *Metasolpuga picta* (Kraepelin) (Solifugae, Solpugidae) compared with that of nocturnal species. J. Arachnol., 14:363–383.

Wilkinson, L. 1984. SYSTAT: The system for statistics. Systat Inc., Evanston, Illinois.

Williams, G.C. 1966. Adaptation and natural selection. Princeton Univ. Press, Princeton, New Jersey.

Winfield, I.J. & C.R. Townsend. 1983. The cost of copepod reproduction : Increased susceptibility to fish predation. Oecologia, 60:406–411.

Fred Punzo: Department of Biology, Box 5F, University of Tampa, 401 W. Kennedy Blvd., Tampa, Florida 33606 USA

RESEARCH NOTE

CHEMICAL ATTRACTION OF CRAB SPIDERS (ARANEAE, THOMISIDAE) TO A FLOWER FRAGRANCE COMPONENT

How crab spiders choose their hunting sites has been investigated in only one species, *Misumena vatia* (Clerck 1757) from North America (Morse & Fritz 1982; Morse 1988, 1993; Greco & Kevan 1994). Morse (1988) and Greco & Kevan (1994) stated that visual and tactile cues are crucial for finding and selecting hunting sites. Although chemical stimuli seem to be important for orientation and behavior of spiders (Tietjen & Rovner 1982; Barth 1993), the importance of chemicals for finding hunting sites has never been tested. However, recently, Aldrich & Barros (1995) reported that male crab spiders of four *Xysticus* Koch 1835 species were attracted by *(E)*-2-Octenal and *(E)*-2-Decenal.

During a project on scarab beetles (Coleoptera, Scarabaeoidea) in the Ivory Coast, we tested whether some lures attract beetles and other arthropods. These experiments were mainly unsuccessful. However, we caught some crab spiders (Thomisidae) with one type of lure, eugenol.

We conducted our experiments in the Parc National de la Comoé in the northeastern Ivory Coast (= Côte d'Ivoire, West Africa) in the Guinea savanna region (Porembski 1991). All traps were situated in the savanna near the gallery forest of the river Comoé near the research camp of the University of Würzburg (Lola Camp; 8°45′08″N, 3°49′02″W). We ran the trapping experiments between 11 June–10 July 1995.

We used pitfall traps, without preservation fluids, made of a blue plastic funnel of about 10 cm diameter placed on the top of a transparent plastic cup (diameter 8 cm, height 10 cm). The bait was placed at the bottom of the funnel. In most of the traps only the lower half was embedded in the ground.

We used eugenol (2-Methoxy-4-(2-propenyl)phenol = 4-allyl-2-methoxy-phenol = 3-(3-methoxy-4-hydroxyphenyl)prop-1-ene) of Fluka Chemie AG, Buchs, Switzerland (purity

≥ 99%; Ch.Nr.: 337412/1-794), 10 drops (14./18.VI.) or 5 drops (19.VI.-04.VII.) on bathroom tissue paper (brand Lotus, made by SATOCI, Abidjan) in each trap. As a control, we use our experiments with other chemicals (anethole, cinnamyl alcohol, geraniol (Fluka), and ethyl chrysanthemumate (ICN, Costa Mesa, California, USA). The spider species were identified by Dr. A. Dippenaar-Schoeman, Institute for Plant Protection, Pretoria. The specimens are deposited in the collection of the Institute for Plant Protection, Pretoria.

In eugenol baited traps we found seven individuals of two species of Thomisidae (Table 1). In contrast, with the control traps, no Thomisidae were caught (Table 2). Since Thomisidae were caught only in traps baited with eugenol, whereas no crab spiders were attracted to control traps, we postulate that eugenol served as an attractant for these spiders. Both *Thomisus blandus* Karsch 1880 and *T. daradoides* Simon 1890 were first recorded from the Ivory Coast by Dippenaar-Schoeman (1983). Only two specimens of *T. blandus* were collected at Zatta (6°52′N, 5°24′W) and Kossou (6°57′N, 4°48′W), and one specimen of *T. daradioides* at Kossou (geographical coordinates according to Office of Geography 1965). No further records from this country are known. Hence, our present records are the second one of *T. daradioides* and the third one of *T. blandus* from Ivory Coast.

Eugenol causes behavioral reactions in many insect species. It serves as a repellent or deterrent to some Coleoptera (Hassanali et al. 1990 [Curculionidae]), Diptera (Girolami et al. 1981 [Tephritidae]; Vartak et al. 1994 [Muscidae, Culicidae]), Lepidoptera (Hattori et al. 1992 [Pyralidae]), and Blattodea (Vartak et al. 1994 [Blattidae]), and as an attractant to Lepidoptera (Dethier 1947: 97 [Tortricidae]), Hymenoptera (Rebêlo & Garófalo 1991 [Apidae] Allsopp 1992 [Scoliidae]), Diptera (Sharma & Saxena 1974 [Muscidae]), and Co-

Table 1.—Species of Thomisidae caught by eugenol traps. Imm. = immature specimen. Date and time of collection in parentheses. Areas: I: at the boundary between gallery forest and savanna. II: savanna about 50 m away from the gallery forest. III: savanna about 100 m away from the gallery forest).

Species/area	I	II	III
Thomisus *daradioides*			1 ♀ (19 June 1995, 1200 h) 1 ♂ (19 June 1995, 1100 h)
Thomisus *blandus*	1 ♀ imm. (29 June 1995, 1145 h) 1 imm. (01 July 1995, 1700 h)	1 imm. (03 July 1995) 1 imm. (04 July 1995)	
Thomisidae sp.			1 spm. (14 June 1995, 1200 h; not conserved)

leoptera (Thomas & Hertel 1969 [Curculionidae]; Hesler et al. 1994 [Chrysomelidae]; Maetô et al. 1995 [Scarabaeidae, Cerambycidae]).

Eugenol is a common essential oil present in plant species of different families all over the world (Gildemeister & Hoffmann 1966: 430ff; Knudsen et al. 1993: 266; Pauli 1994: 26). Since it is often a component of flower fragrances, it could be directly associated with the hunting sites of those crab spiders species which are waiting on flowers for prey.

According to Dippenaar-Schoeman (1983), both *Thomisus blandus* and *T. daradioides* were collected mainly from flowers. Hence, they probably use flowers as hunting sites. Thus, the ability to use a flower fragrance component as an attractant would be an advantage for these species in finding their hunting sites.

The present record is the first indication of attraction of Thomisidae to a floral fragrance component. The above-mentioned aldehydes *(E)*-2-Octenal and *(E)*-2-Decenal that attract Thomisidae may be identical to or components of the pheromones of the *Xysticus* females (Aldrich & Barros 1995) or else, being the main components of the defensive secretions of bugs (Heteroptera), may indicate the

presence of a potential prey. Eugenol, however, gives an indirect information about the presence of a potential prey to the spiders by indicating the prey's feeding place, a fragrant flower.

LITERATURE CITED

Aldrich, J.R. & T.M. Barros. 1995. Chemical attraction of male crab spiders (Araneae, Thomisidae) and kleptoparasitic flies (Diptera, Milichiidae and Chloropidae). J. Arachnol., 23:212–214.

Allsopp, P.G. 1992. Volatile compounds as attractants for *Cymsomeris tasmaniensis* (Saussure) (Hymenoptera: Scoliidae). Australian Entomol. Mag., 19:107–110.

Barth, F.G. 1993. Sensory guidance in spider precopulatory behaviour. Comp. Biochem. Physiol., 104A:717–733.

Dethier, V.G. 1947. Chemical insect attractants and repellents. Blakiston Company, Philadelphia and Toronto. 289 pp.

Dippenaar-Schoeman, A.S. 1983. The spider genera *Misumena*, *Misumenops*, *Runcinia* and *Thomisus* (Araneae: Thomisidae) of southern Africa. Entomology Mem. Dep. Agric. Repub. South Africa, 55:66 pp.

Gildemeister, E. & F. Hoffmann. 1966. Die äther-

Table 2.—Trapping time and captured Thomisidae specimens. Others: anethole, cinnamyl alcohol, geraniol: 1702 h each; ethyl chrysanthemumate: 124 h.

Lure	Trapping time	Specimens
eugenol	2629 h	7
others	5714 h	0

ischen Öle. Band IIId. 4. Aufl. (Bearb. D. Merkel). Akademie-Verlag, Berlin. XXIII + 902 pp.

Girolami, V., A. Vianello, A. Strapazzon, E. Ragazzi & G. Veronese. 1981. Ovipositional deterrents in *Dacus oleae*. Entomol. Exp. Appl., 29: 177–188.

Greco, C.F. & P.G. Kevan. 1994. Contrasting patch choosing by anthophilous ambush predators: vegetation and floral cues for decision by a crab spider (*Misumena vatia*) and males and females of an ambush bug (*Phymata americana*). Canadian J. Zool., 72:1583–1588.

Hassanali, A., W. Lwande, N. Ole-Sitayo, L. Moreka, S. Nokoe & A. Chapya. 1990. Weevil repellent constituents of *Ocimum suave* leaves and *Eugenia caryophyllata* cloves used as grain protectants in parts of Eastern Africa. Discov. Innov., 2:91–95.

Hattori, M., Y. Sakagami & S. Marumo. 1992. Oviposition deterrents for the limabean pod borer, *Etielle zinckenella* (Treitschke) (Lepidoptera: Pyralidae) from *Populus nigra* L.c.v. Italica leaves. Appl. Entomol. Zool., 27:195–204.

Hesler, L.S., D.R. Lance & G.R. Sutter. 1994. Attractancy of volatile non-pheromonal semiochemicals to northern corn rootworm beetles (Coleoptera: Chrysomelidae) in eastern South Dakota. J. Kans. Entomol. Soc., 67:186–192.

Knudsen, J.T., L. Tollsten & L.G. Bergström. 1993. Floral scents - A checklist of volatile compounds isolated by head-space techniques. Phytochemistry, 33:253–280.

Maetô, K., K. Fukuyama, A.S. Sajap & Y.A. Wahab. 1995. Selective attraction of flower-visiting beetles (Coleoptera) to floral fragrance chemicals in a tropical rain forest. Japanese J. Entomol., 63: 851–859.

Morse, D.H. 1988. Cues associated with patch-choice decisions by foraging crab spiders *Misumena vatia*. Behaviour, 107:297–313.

Morse, D.H. 1993. Choosing hunting sites with little information: patch-choice responses of crab spiders to distant cues. Behav. Ecol., 4:61–65.

Morse, D.H. & R.S. Fritz. 1982. Experimental and observational studies of patch choice at different

scales by the crab spider *Misumena vatia*. Ecology, 63:172–182.

Office of Geography. 1965. Ivory Coast. Official standard names approved by the U.S. Board on Geographic Names. Washington. 250 pp.

Pauli, A.H.A. 1994. Chemische, physikalische und antimikrobielle Eigenschaften von in ätherischen Ölen vorkommenden Phenylpropanen. Thesis (Dr. rer. nat.), Julius-Maximilians-Universität Würzburg. [8] + 236 + 139 pp.

Porembski, S. 1991. Beiträge zur Pflanzenwelt des Comoé-Nationalparks (Elfenbeinküste). Natur und Museum, Frankf. a. M., 121:61–83.

Rebêlo, J.M.M. & C.A. Garófalo. 1991. Diversidade e sazonalidade de machos de Euglossini (Hymenoptera, Apidae) e preferências por iscas-odores em um fragmento de floresta no sudeste do Brasil. Rev. Brasileira Biol., 51:787–799.

Sharma, R.N. & K.N. Saxena. 1974. Orientation and developmental inhibition in the housefly by certain terpenoids. J. Med. Entomol., 11:617–621.

Tietjen, W.J. & J.S. Rovner. 1982. Chemical communication in lycosids and other spiders. Pp. 249–279. *In* Spider Communication. Mechanisms and Ecological Significance. (P.N. Witt & J.S. Rovner, eds.). Princeton Univ. Press, Princeton, New Jersey.

Thomas, H.A. & G.D. Hertel. 1969. Responses of the pales weevil to natural and synthetic host attractants. J. Econ. Entomol., 62:383–386.

Vartak, P.H., V.B. Tungikar & R.N. Sharma. 1994. Comparative repellent properties of certain chemicals against mosquitoes, house flies and cockroaches using modified techniques. J. Com. Dis., 26:156–160.

Frank-Thorsten Krell and **Franziska Krämer**: Theodor-Boveri-Institut für Biowissenschaften der Universität Würzburg, Lehrstuhl Zoologie III, Am Hubland, D-97074 Würzburg, Germany.

RESEARCH NOTE

NOTES ON THE SYSTEMATICS OF THE LITTLE KNOWN THERAPHOSID SPIDER *HEMIRRHAGUS CERVINUS*, WITH A DESCRIPTION OF A NEW TYPE OF URTICATING HAIR

The presence of urticating hairs as a tarantula defense mechanism is so far restricted to the New World Theraphosidae. The irritation caused by these hairs has been known since Bates (1863) but not formally characterized until Cooke et al. (1972) described four types of abdominal urticating hairs. Marshall & Uetz (1990) described a fifth type of urticating hair from *Ephebopus* sp. which is found on the prolateral surface of palpal femur, rather than the abdomen. The defensive behavior involved in the release of abdominal urticating hairs was studied in detail by Pérez-Miles & Prandi (1991) in the Theraphosinae *Phrixotrichus mollicoma* (Ausserer 1875) (previously *Grammostola mollicoma*) and by Bertani & Marques (1995/96) in several species of Theraphosinae and Aviculariinae.

Urticating hairs and the associated releasing behavior was used by Pérez-Miles (1992, 1995) and Pérez-Miles et al. (1996) to elucidate phylogenetic relationships in the Theraphosinae and related groups. Since defensive abdominal movements are present only in the Aviculariinae and Theraphosinae, this was interpreted as a synapomorphy, supporting their sister group relationship (Pérez-Miles et al. 1996). However, Theraphosinae shed small urticating hairs while Aviculariinae (except *Ephebopus* Simon 1892) employ larger urticating hairs by direct contact with the potential predator. Considering the differences in morphology and release mechanisms of the urticating hairs in the Aviculariinae versus the Theraphosinae, their independent acquisition was proposed (Pérez-Miles 1995; Pérez-Miles et al., 1996; Bertani & Marques 1995/96). The different location of urticating hairs of *Ephebopus* also suggests their independent evolution (Bertani & Marques 1995/96).

Hemirrhagus cervinus (Simon 1891) has a distinct pad of urticating hairs on the dorsal surface of the abdomen. Scanning electron microscopy revealed that they differ in morphology and arrangement from known types of theraphosid urticating hairs. *H. cervinus,* the type species of the genus, is only known from the holotype specimen. The genus has a controversial systematic position. Raven (1985) considered it as a Theraphosidae *incertae sedis.* Smith (1994) recommended suspending the genus because he thought the type lost. Only The International Commission on Zoological Nomenclature has power to suppress a name, ICZN art. 79. The female holotype of *Hemirragus cervinus,* from Mexico, deposited at the Museum National d'Histoire Naturelle de Paris, is available and was examined. To minimize the damage to the type, a small area (less than 1 mm^2) of the dorsal surface of the abdomen bearing hairs was removed for study by SEM and some loose hairs were observed by light microscopy. Other characters were studied by a stereoscopic microscope, drawings were made with the aid of a camera lucida. Considering the size and morphology of abdominal urticating hairs in *H. cervinus,* the releasing mechanism seems to be as in Theraphosinae (hair flicking–airborne dispersal). The presence of such urticating hairs lead me to propose the placement of *H. cervinus* in the Theraphosinae.

Abdominal hair morphology.—Scanning electron micrographs reveal straight, stout fusiform barbed hairs, acutely pointed at both ends (Figs. 1–4). The length of these hairs is 0.315 ± 0.021 mm (mean ± 1 SD, $n = 30$ hairs). Hair barbs are subtriangular but not homogeneous in size, and slightly longer on the distal region. Barbs, present on the proximal
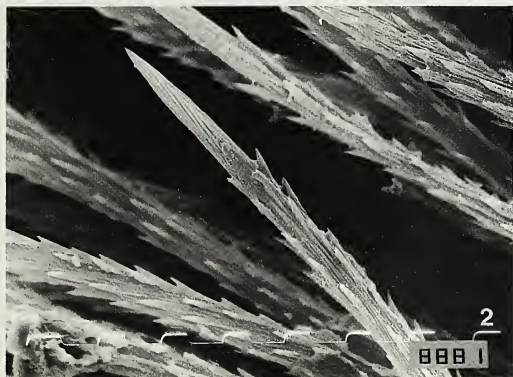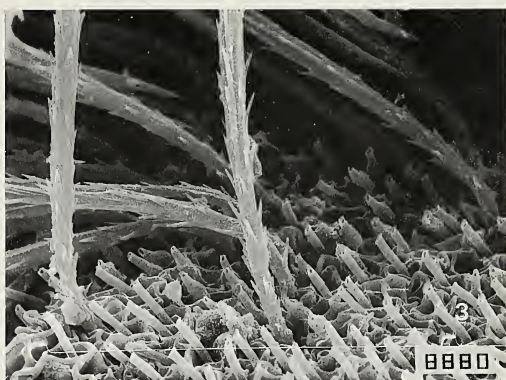
Figures 1, 2.—Scanning electron micrographs of abdominal hairs of *Hemirrhagus cervinus*. 1, Structure of the urticating hairs, hair field partially ablated showing arrangement of the hairs (Scale = 0.2 mm); 2, Close up of the distal portion of an urticating hair (Scale = 0.02 mm).

Figures 3, 4.—Scanning electron micrographs of abdominal hairs of *Hemirrhagus cervinus*. 3, Close up of the cuticle showing the basal part of attached hairs and ablated hair sockets (Scale = 0.2 mm); 4, Close up of the basal end of some loose urticating hairs, showing the acute basal tip out of the socket (Scale = 0.02 mm).

80% of the hair, are obliquitous with respect to the hair axis (40°), and orientated with their tips towards the hair distal end (Fig. 2). A slight inflection of approximately 5–10° was observed in the axis of some hairs, near the proximal bases.

Abdominal hairs are attached in distinctive insertion sockets on the cuticle (Fig. 3). The sockets are cylindrical and the bases of the hairs are held in them until the hair is released. The region of the hair that is located in the socket is not barbed and has a very sharp tip (Fig. 4).

SYSTEMATICS

Hemirrhagus cervinus (Simon 1891)

Cratorrhagus cervinus Simon 1891:330; F. Pickard-Cambridge 1899:41; *Hemirrhagus cervinus* Simon 1903:926; Strand 1907:16, 1912:175; Petrunkevitch 1911:71, 1928:78; Roewer 1942:231; Raven 1985:116; Smith 1994:185.

Holotype.—Female from Mexico, without locality data, deposited in Museum National d'Histoire Naturelle, Paris, #756, examined.

Diagnosis.—Differs from other Theraphosidae by the presence of urticating hairs of the type described here (Figs. 1–4), in the coxae with a retrolateral-ventral heel (Fig. 5), and in the morphology of the spermathecae (Fig. 6). It differs from the Aviculariinae in the different morphology of the scopulae (not laterally extended), scopular hairs (not widely spatulate), and urticating hairs.

Comments.—Morphological and positional evidence presented here suggests that the defensive function and urticating effect of abdominal hairs of *H. cervinus* is similar to those found in other New World theraphosids. Hair flicking seems likely to be the shedding mechanism, considering their small size (0.315 mm, length) and their presumed low
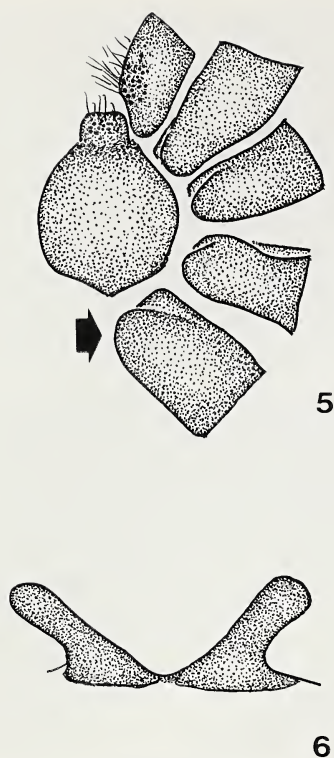
Figures 5, 6.—Structures of the holotype of *Hemirrhagus cervinus*. 5, Ventral view of labium, sternum and left coxae showing the retrolateral projection on coxae of all legs (arrow shows this feature only on coxa of fourth leg); 6, Spermathecae, ventral view.

weight in comparison with larger (0.5–1.5 mm, length), heavier urticating hairs from arboreal Aviculariinae (Bertani & Marques 1995/96) which rely on contact, not airborne dispersal.

Both distal and basal ends of the hair are sharp, but the orientation of the barbs suggests that the penetration tip is the basal end. The orientation of the barbs and the socket morphology of type V hairs (from fig. 2 of Marshall & Uetz 1990) led me to assume that the penetrating end lies proximally, which agrees with Bertani & Marques (1995/96). A proximal position of the penetrating tip was also indicated for hairs of type II (Cooke et al. 1972; Bertani & Marques 1995/96); but considering the differences in morphology, arrangement, and shedding mechanisms with *Hemirrhagus*, that similarity is interpreted as nonhomologous.

The type of abdominal hairs found on *H.*

cervinus is morphologically similar to those of *Ephebopus*, but shorter. Also the socket is narrower and the main difference is their location on the body. For these reasons abdominal hairs of *Hemirrhagus* cannot be considered as homologous to the palpal hairs of *Ephebopus*. These facts suggest that the urticating hairs found in *Hemirrhagus* are of a 6th, previously undescribed, type.

Hemirrhagus, traditionally placed in Ischnocolinae (Ischnocoleae of Simon 1903, in Ischnocolinae by Roewer 1942), and was considered as Theraphosidae *incertae sedis* by Raven (1985). The examination of the type and the study of some features lead me to propose the placing of *Hemirrhagus* in the Theraphosinae.

Hemirrhagus cervinus has abdominal urticating hairs, which are only found in Theraphosinae and Aviculariinae. *H. cervinus* does not have wide scopulae, lacks spatulate scopula hairs, and lacks the heavy, contact urticating hairs as they occur in the Aviculariinae. Also, leg spines are absent or scarce in Aviculariinae, but are present in *H. cervinus*. All these facts argue against its inclusion in the Aviculariinae. Pérez-Miles et al. (1996) proposed the abdominal defensive movements as synapomorphic of Aviculariinae plus Theraphosinae. Since *H. cervinus* is only known from the type, this could not be tested. However, the presence of abdominal urticating hairs suggests such behavior. If this hypothesis is correct then its inclusion in Theraphosinae seems to be the best placement, at least until the male is described. The spermathecal morphology is compatible with the proposed placement. Also the coxae of legs with retrolateral projection indicated by Smith (1994) is here confirmed in the type, and interpreted as a generic apomorphy.

ACKNOWLEDGEMENTS

LITERATURE CITED

Bates, H.W. 1863. The Naturalist on the river Amazons. Vol. 1, John Murray, London, Pp. 160–162.

Bertani, R. & O.A.V. Marques. 1995/96. Defensive behaviors in Mygalomorph spiders: release of urticating hairs by some Aviculariinae (Araneae, Theraphosidae). Zool. Anz., 234:161–165.

Cooke, J.A.L., V.D. Roth & F.H. Miller. 1972. The urticating hairs of theraphosid spiders. American Mus. Nov., 2498:1–43.

Intern. Comm. Zool. Nomen.. 1985. Intern. Code Zool. Nomen., 3rd ed., Intern. Trust Zool. Nomen., London, 338 pp.

Lucas, S., P.I. da Silva, Jr. & R. Bertani. 1991. The genus *Ephebopus* Simon, 1892. Description of the male of *Ephebopus murinus* (Walckenaer), 1837. (Araneae, Theraphosidae, Aviculariinae). Spixiana, 14(3):245–248.

Marshall, S.D. & G.W. Uetz. 1990. The pedipalpal brush of *Ephebopus* sp. (Araneae, Theraphosidae): Evidence of a new site for urticating hairs. Bull. British Arachnol. Soc., 8(4):122–124.

Pérez-Miles, F. 1992. Análisis cladístico preliminar de la subfamilia Theraphosinae (Araneae, Theraphosidae). Bol. Soc. Zool. Uruguay, 7:11–12.

Pérez-Miles, F. 1995. Revisión y análisis cladístico de la subfamilia Theraphosinae (Araneae, Mygalomorphae, Theraphosidae). Ph.D. thesis, Universidad de la República, Montevideo.

Pérez-Miles, F., S.M. Lucas, P.I. da Silva, Jr. & R. Bertani. 1996. Systematic revision and cladistic analysis of Theraphosinae (Araneae: Theraphosidae). Mygalomorph, 1:33–66.

Pérez-Miles, F. & L. Prandi. 1991. El comportamiento de emisión de pelos urticantes en *Grammostola mollicoma* (Araneae, Theraphosidae): un análisis experimental. Bol. Soc. Zool. Uruguay, 6:47–53.

Raven, R.J. 1985. The spider infraorder Mygalomorphae (Araneae): cladistics and systematics. Bull. American Mus. Nat. Hist., 182:1–180.

Smith, A.W. 1994. Tarantula spiders, Vol. 2. Tarantulas of the U.S.A. and Mexico. Fitzgerald Publ., London, 196 pp.

Fernando Pérez-Miles: División Zoología Experimental, Instituto de Investigaciones Biológicas Clemente Estable, Av. Italia 3318, 11600 Montevideo, Uruguay; and Sección Entomología, Facultad de Ciencias, T. Narvaja 1674, 11200 Montevideo, Uruguay

ARACHNOLOGICAL RESEARCH FUND

The AAS Fund for Arachnological Research (AAS Fund) is funded and administered by the American Arachnological Society. The purpose of the fund is to provide research support for work relating to any aspect of the behavior, ecology, physiology, evolution, and systematics of any of the arachnid groups. Awards may be used for field work, museum research (including travel), expendable supplies, identification of specimens, and/or preparation of figures and drawings for publication. Monies from the fund are not designed to augment or replace salary.

Individual awards will not exceed $1000.00, and, although open to all students and faculty with less than $500.00 per year research budget, preference will be given to students. A total of $6000.00 is available for awarding during each funding year. Available monies could be expended for three large proposals, a greater number of partially funded proposals, and/or a number of smaller, less expensive proposals. The final funding pattern is at the discretion of the review committee.

Applications for support should be received by the chair of the review committee no later than October 31. To be considered for an award from the AAS Fund, please submit four copies of a proposal of no more than five pages (including references) detailing your research project.

Proposals should have three main parts: 1) an INTRODUCTION where background information is presented relative to the proposed work. The introduction should include a section which places the proposed work in context with currently known relevant information, a section which provides justification for the proposed work, and a clear statement of the hypothesis(ses) to be tested, or, in the case of systematic revisions, the type of synthesis that will be achieved and its significance; 2) a METHODS section where the methods, materials, experimental design, and statistical or taxonomic analysis(ses) to be used are clearly and concisely presented, and 3) a BUDGET explaining (in detail) how monies awarded will be spent in the proposed research.

Proposals should be submitted to:

Dr. Deborah Smith, AAS Fund Chair
Department of Entomology
Haworth Hall
University of Kansas
Lawrence, KS 66045 USA

Proposals must be submitted in English. The four copies of the proposal must be in the hands of the Fund chair by the appropriate deadlines to be considered. Electronic submission and/or FAX submission of proposals with hard copies to follow is acceptable only if the other copies arrive before the stated deadlines. If these submission rules are difficult or prohibitive because of cost, erratic postal services, or remote location (remote field stations or sites), other methods of submission may be acceptable. For other submission possibilities, please contact the chair of the Fund at the above address, or electronically at dsmith@kuhub.cc.ukans.edu. Alternative submissions will be accepted only if the chair has been previously contacted, and all deadlines will still apply.

INSTRUCTIONS TO AUTHORS

(revised October 1996)

Manuscripts are preferred in English but may be accepted in Spanish, French or Portuguese subject to availability of appropriate reviewers. Authors whose primary language is not English may consult the Associate Editor for assistance in obtaining help with English manuscript preparation. All manuscripts should be prepared in general accordance with the current edition of the *Council of Biological Editors Style Manual* unless instructed otherwise below. Authors are advised to consult a recent issue of the *Journal of Arachnology* for additional points of style. Manuscripts longer than 1500 words should be prepared as Feature Articles, shorter papers as Research Notes. Send **four** identical copies of the typed material together with photocopies of illustrations to the **Managing Editor.** Do not send original handmade illustrations until the manuscript has been accepted. Mail to:

Petra Sierwald, Managing Editor; Division of Insects, Dept. of Zoology, Field Museum, Roosevelt Road at Lakeshore Drive, Chicago, IL 60605 USA [Telephone: (312) 922-9410, ext. 841; FAX: (312) 663-5397; E-mail: SIERWALD@FMNH.ORG]

Correspondence relating to the initial submission of a manuscript, as well as the review process, should be directed to the Associate Editor. Correspondence relating all other matters should be directed to the Editor. After the manuscript has been accepted, the author will be asked to submit the manuscript on a computer disc. It must be in a widely used program (preferably in MS DOS WordPerfect). Indicate clearly on the computer disc the word processing program used.

FEATURE ARTICLES

Title page.—The title page will include the complete name, address, and telephone number of the author with whom proofs and correspondence should be exchanged, a FAX number and electronic mail address if available, the title in capital letters, and each author's name and address, and the running head (see below).

Abstract.—The heading in capital letters should be placed at the beginning of the first paragraph set off by a period. In articles written in English, a second abstract in an acceptable language may be included pertinent to the nationality of the author(s) or geographic region(s) emphasized in the article. A second abstract in English must be included in articles not written in the latter language.

Text.—Double-space text, tables, legends, etc. throughout. Three levels of heads are used. The first level (METHODS, RESULTS, etc.) is typed in capitals and on a separate line. The second level head begins a paragraph with an indent and is separated from the text by a period and a dash. The third level may or may not begin a paragraph but is italicized and separated from the text by a colon. Use only the metric system unless quoting text or referencing collection data. All decimal fractions are indicated by the period regardless of language of the text.

Citation of references in the text: Cite only papers already published or in press. Include within parentheses the surname of the author followed by the date of publication. A comma separates multiple citations by the same author(s) and a semicolon separates citations by different authors, e.g., (Smith 1970), (Jones 1988; Smith 1993), (Smith 1986, 1987; Smith & Jones 1989; Jones et al. 1990).

Literature cited section.—Use the following style:

Lombardi, S. J. & D. L. Kaplan. 1990. The amino acid composition of major ampullate gland silk (dragline) of *Nephila clavipes* (Araneae, Tetragnathidae). J. Arachnol., 18:297–306.

Krafft, B. 1982. The significance and complexity of communication in spiders. Pp. 15–66, *In* Spider

Communications: Mechanisms and Ecological Significance. (P. N. Witt & J. S. Rovner, eds.). Princeton University Press, Princeton, New Jersey.

Footnotes.—Footnotes are permitted only on the first printed page to indicate current address or other information concerning the author. All footnotes are placed together on a separate manuscript page.

Running head.—The author surname(s) and an abbreviated title should be typed all in capital letters and must not exceed 60 characters and spaces. The running head should be placed near the top of the title page.

Taxonomic articles.—Consult a recent taxonomic article in the *Journal of Arachnology* for style or contact the Editor.

Tables.—Each table, with the legend above, should be placed on a separate manuscript page. Only horizontal lines (usually three) should be included. Use no footnotes; instead, include all information in the legend. Make notations in the text margins to indicate the preferred location of tables in the printed text.

Illustrations.—Address all questions concerning illustrations to:

James W. Berry, Editor; Dept. of Biological Sciences, Butler University, Indianapolis, Indiana 46208 USA [Telephone (317) 940-9344; FAX (317) 940-9519; E-mail: jwberry@thomas.butler.edu]

All art work must be camera-ready for reproduction. In line drawings, pay particular attention to width of lines and size of lettering when reductions are to be made by the printer. Multiple photos assembled on a single plate should be mounted with only a minimum of space separating them. In the case of multiple illustrations mounted together, each illustration must be numbered sequentially rather than given an alphabetic sequence. Written on the back should be the name(s) of author(s) and an indication of top edge. The author should indicate whether the illustrations should be one column or two columns in width. The overall dimensions of original artwork should be no more than 11 inches (28 cm) × 14 inches (36 cm). Photocopies in review manuscripts should be reduced to the exact measurements that the author wants to appear in the final publication. Larger drawings present greater difficulty in shipping and greater risks of damage for which the JOA assumes no responsibility. Make notations in the text margins to indicate the preferred position of illustrations in the printed text.

Legends for illustrations should be placed together on the same page(s) and separate from the illustrations. Each plate must have only one legend, as indicated below:

Figures 1–4.—*A-us x-us*, male from Timbuktu. 1, Left leg; 2, Right chelicera; 3, Dorsal aspect of genitalia; 4, Ventral aspect of abdomen.

Figures 27–34.—Right chelicerae of species of *A-us* from Timbuktu. 27, 29, 31, 33, Dorsal views; 28, 30, 32, 34, Prolateral views of moveable finger; 27, 28, *A-us x-us,* holotype male; 33, 34, *A-us y-us,* male. Scale = 1.0 mm.

Assemble manuscript for mailing.—Assemble the separate sections or pages in the following sequence: title page, abstract, text, figure legends, footnotes, tables with legends, figures.

Page charges, proofs and reprints.—There are no page charges, but authors will be charged for changes made in the proof pages. Authors will receive a reprint order form along with their page proofs. Reprints will be billed at the printer's current schedule of costs.

RESEARCH NOTES

Instructions above pertaining to feature articles apply also to research notes, except that abstracts and most headings are not used and the author's name and address follow the Literature Cited section.

CONTENTS

The Journal of Arachnology

The Journal of
ARACHNOLOGY

OFFICIAL ORGAN OF THE AMERICAN ARACHNOLOGICAL SOCIETY

VOLUME 26   **1998**   **NUMBER 2**

Cover photo: Web of *Hypochilus thorellii* Marx in the Cumberland Mountains of Tennessee. The webs are built on overhanging rock surfaces and have a characteristic "lampshade" structure. Photo by Alan Cady.

THE SPIDER GENUS *NAPOMETA*
(ARANEAE, ARANEOIDEA, LINYPHIIDAE)

Gustavo Hormiga: Department of Biological Sciences, George Washington University, Washington, D.C. 20052 USA

ABSTRACT. The spider genus *Napometa* Benoit, which had been erroneously placed in the Metinae (Tetragnathidae), is transferred to the family Linyphiidae. The only two known species of *Napometa*, *N. sanctaehelenae* and *N. trifididens*, are redescribed and illustrated.

The spider genus *Napometa* was erected by Benoit (1977) to include two species from St. Helena island, in the South Atlantic Ocean: *N. sanctaehelenae* Benoit 1977 and *N. trifididens* (O. Pickard-Cambridge 1873). Benoit designated *N. sanctaehelenae* as the type species of this new genus within the then araneid subfamily Metinae (currently a subfamily within Tetragnathidae; see Hormiga et al. (1995) for a summary of the taxonomic history of the separation of Araneidae and Tetragnathidae). *N. trifididens*, originally described by Pickard-Cambridge as a linyphiid, had been in the theridiid genus *Enoplognatha* Pavesi 1880 (Simon 1894) for three-quarters of a century when Benoit transferred it to *Napometa*. Since then no other species have been described within *Napometa*, and the genus is currently listed as a member of the family Tetragnathidae (Platnick 1993; Dippenaar-Schoeman & Jocqué 1997).

The male palp illustrations that accompanied Benoit's description of *Napometa* cast some serious doubts about its familial assignment. Benoit's ventral (figs. 76a, 77c) and mesal (fig. 76b) views of the male palp resemble a typical linyphiid, with the U-shaped intersegmental paracymbium and the suprategular apophysis clearly depicted. Examination of Benoit's specimens confirms that *N. sanctaehelenae* and *N. trifididens* are in fact linyphiids, not tetragnathids nor araneids.

Benoit's descriptions of *Napometa* species focused almost exclusively on somatic morphology, with little attention to the details of the genitalic morphology. The purpose of this paper is to transfer *Napometa* to its correct familial placement (Linyphiidae) and describe and illustrate in more detail the genitalic mor-

phology of *N. sanctaehelenae* and *N. trifididens*. The somatic morphology is also illustrated to complement Benoit's detailed description.

METHODS

General methods of study are described in Hormiga (1994a). The morphological observations were carried out using a Leica MZA-PO dissecting microscope and a Leica DMRM compound microscope. For examination of the genitalic structures under transmitted light microscopy the specimens were immersed in methyl salicylate (Holm 1979) and mounted using Coddington's (1983) temporary slide mounting method. All illustrations were done using a camera lucida and inked on drafting film or coquille board. All measurements are in millimeters. Abbreviations are listed in Table 1.

TAXONOMY

Linyphiidae Blackwall 1859
Napometa Benoit 1977

Napometa Benoit 1977: 185. Type species, by original designation, *Napometa sanctaehelenae* Benoit 1977. Brignoli 1983: 230. Platnick 1989: 299. Platnick 1993: 377. Dippenaar-Schoeman & Jocqué 1997: 292, 338.

Etymology.—Benoit did not explain the etymology of *Napometa*. Presumably he derived this name from the tetragnathid genus *Meta* Koch 1836. As for the *Napo-* prefix, Don Cameron (*in litt.*) suggests that it is derived from Napoleon, the most famous resident of the type locality, St. Helena. Thus, Benoit may have intended to convey with this name "Napoleon's *Meta*."

Diagnosis.—*Napometa* differs from other

Table 1.—Anatomical abbreviations used in the figures.

A	Alveolus
CD	Copulatory duct
CO	Copulatory opening
E	Embolus
EM	Embolic membane
FD	Fertilization duct
m	Membrane (or membranous)
LC	Lamella characteristica
P	Paracymbium
S	Spermatheca
SA	Suprategular apophysis
SPT	Suprategulum
ST	Subtegulum
T	Tegulum
TA	Terminal apophysis

linyphiids by the following combination of characters: cymbium with "free" pointed apex (Fig. 1); U-shaped intersegmental para-cymbium with broad proximal arm; embolus short, not thread-like, with blunt apical end; large lamella characteristica with a conspicuous, caudally directed, pointed process (Figs. 3, 15). Terminal apophysis with a single coil and a hollow axis (Fig. 3). Epigynum (*N. trifididens* females are unavailable for study) with a small dorsal plate scape with a socket (Fig. 6); epigynal copulatory openings small and inconspicuous.

Description.—*Male:* Clypeus height 5–6× an anterior median eye diameter (Figs. 11, 17). Chelicerae large, with 5–8 prolateral and 5 retrolateral teeth; stridulatory organ absent. Trichobothrium metatarsus IV absent. Palp (Figs. 1–3, 11, 12): patella short, with a dorsal macroseta. Tibia almost as long (*ca.* 75–80%) as the cymbium; one or two prolateral and two or three retrolateral trichobothria and one ectal macroseta. Cymbium with pointed apex; alveolus occupying the basal ⅔ of the cymbium, leaving the distal ⅓ "free." Paracymbium U-shaped, attached by means of a membrane to the cymbium base, the proximal arm being much wider than the tapered distal arm. Tegulum with an apical lobe. Suprategular apophysis hook-shaped, visible in ectal and ventral views, distad of the tegular lobe. Embolus partially visible, in ectal view, between the suprategular apophysis, tegular lobe and apical process of the lamella; apical end of embolus blunt. Two membranes associated with the

embolus are visible between the suprategular apophysis and the apical process of the lamella; one of them seems to be attached to the lamella and the other seems to be true embolic membrane (*sensu* Hormiga 1994b; this homology statement requires confirmation by dissecting the embolic division when more specimens become available). Terminal apophysis with a single coil and a hollow axis. Lamella large (about ⅔ of the cymbium length) with a long and pointed posterior process.

Female: See under *Napometa sanctaehelenae* (*N. trifididens* females are unavailable for study; therefore, the description of the females of the genus has to be based on the females of the type species only).

Composition.—Two species, *Napometa sanctaehelenae* Benoit and *N.* trifididens (O. Pickard-Cambridge).

Distribution.—Endemic to St. Helena island.

Napometa sanctaehelenae Benoit 1977
Figs. 1–13

Napometa sanctaehelenae Benoit 1977: 185–187, figs. 76a–g 'ob♂ ♀]. - Brignoli 1983: 230.

Types.—Female holotype from St. Helena, labels state "Napometa sanctaehelenae Benoit ♀ HOLOTYPE; DET. P.L.G. Benoit 1970; LOC. Ste. Hélène Centre: High Central Ridge 2600/2700 ft. 17/XII/1965; REC. P. Basilewsky, P. Benoit, N. Leleup; R.G. Mus. Afr. Centr. 129.143," "Mission Zoologique Belge 1965/66 (P. Basilewsky, P. Benoit, N. Leleup)" and "MT 129.143." Female paratypes from St. Helena, labels state "Napometa sanctaehelenae Benoit ♀ PARATYPES; DET. P.L.G. Benoit 1970; LOC. Ste. Hélène Centre: High Central Ridge, Cabbage Tree Road 2500 ft.; REC. J. Decelle, N. et J. Leleup IV/1967; R.G. Mus. Afr. Centr. 133.388," "Mission Zoologique Belge 1965/66 (P. Basilewsky, P. Benoit, N. Leleup)," "Det. P.L.G. Benoit 1970 ♀ Napometa sanctaehelenae n. sp. paratypes" and "MT 133.388" (3 ♀ & 3 juveniles; one of the epigyna is missing). Male paratype from St. Helena, labels state "Napometa sanctaehelenae Benoit ♂ Allotype; DET. P.L.G. Benoit 1970; LOC. Ste. Hélène Centre: High Central Ridge 17/XII/1965; REC. P. Basilewsky, P. Benoit, N. Leleup; R.G. Mus. Afr. Centr. 136.386," "Det. P.L.G. Benoit 1970 Napometa sanctaehelenae n. sp. ♂ allotype"

and "MT 136.386." All types are deposited at the Royal Museum for Central Africa (Tervuren) and have been examined.

Diagnosis.—The male of *N. sanctaehelenae* can be distinguished from that of *N. trifididens* by the anteromesal process with three cheliceral teeth found in the latter species but not in the former (Figs. 12, 17). The distal arm of the paracymbium of *N. sanctaehelenae* (Fig. 1) is narrower than that of *N. trifididens* (Fig. 14). The anteroectal process of the lamella, as seen in a mesal view, is long and pointed in *N. sanctaehelenae* (Fig. 2) and is flat in *N. trifididens* (Fig. 15). The number of pedipalpal tibia trichobothria is also different between these two species: two prolateral and three retrolateral in *N. sanctaehelenae* versus one prolateral and two retrolateral in *N. trifididens* (Figs. 1, 14).

Description.—*Male (paratype):* Abdomen and cephalothorax are illustrated in Figs. 11–13. Measurements and a detailed description of the male and female somatic morphology are provided by Benoit (1977). Total length 5.15. Cephalothorax 2.15 long, 1.60 wide; abdomen 3.10 long, 1.58 wide. Chelicerae with 7–8 prolateral and 5 retrolateral teeth. Palp (Figs. 1–3): Tibia almost as long (*ca.* 75%) as the cymbium; two prolateral and three retrolateral trichobothria. Cymbium with three mesal and one dorsal macrosetae. Lamella with a pointed ectodistal process, a blunt mesal process, a rounded projection on the mesodorsal margin, and a long and pointed posterior process.

Female (paratype): Abdomen and cephalothorax are illustrated in Figs. 9, 10. Total length 6.80. Cephalothorax 2.64 long, 1.78 wide; abdomen 3.88 long, 3.12 wide. Chelicerae with 8–9 prolateral and 8 retrolateral teeth (Benoit's depiction of the female prolateral teeth, his figure 76d, is not entirely accurate; see Fig. 10). Pedipalp with tarsal claw. Trichobothrium metatarsus I 0.15. Posterior lateral spinnerets with enlargement of the peripheral cylindrical silk gland spigot base.

Epigynum (Figs. 4–8): slightly broader than long, protruding very little from the abdominal wall. Dorsal plate with a small scape (somewhat exaggerated in Benoit's fig. 76f) with a shallow socket. Benoit's illustration of the vulva (fig. 76g) is inaccurate (compare to Fig. 7). The copulatory openings are located on both sides of the dorsal plate, near the lateral plate (Figs. 7, 8). There is no clear distinction between the end of the copulatory duct and the beginning of the spermatheca. The copulatory duct spirals around the fertilization duct, the latter changes from a ventral into a dorsal position by turning around the proximal end of the former (i.e., near the copulatory opening).

Distribution.—Known only from St. Helena island.

Material examined.—Only the type series.

Napometa trifididens (O. Pickard-Cambridge 1873)
Figs. 14–17

Linyphia trifididens, - O. Pickard-Cambridge 1873: 220–222.
Linyphia trifidens, - Melliss 1875: 212 (*lapsus calami*).
Leptyphantes trifidens, - Simon 1883: 306, 311.
Enoplognatha trifidens, - Simon 1894: 578.
Enoplognatha trifididens, - Roewer 1942: 402. - Bonnet 1956: 48.
Napometa trifididens, - Benoit 1977: 187–188, figs. 77a-c [♂]. - Platnick, 1993: 377–378.

Types.—According to Benoit (1977) the original type series studied by O. Pickard-Cambridge consisted of 3♂ (two of them adults) and 1♀, but only 1♂ remains deposited in The Oxford University Museum; the other ♀ & ♂ are presumably lost. To my knowledge no female specimens of this species are available for study. I have not examined the mentioned type, studied by Benoit, to compare, identify and describe the only other male specimen available in collections. My descriptions are based upon only that other specimen.

Diagnosis.—The male of *Napometa trifididens* can be distinguished from that of *N. sanctaehelenae* by the anteromesal cheliceral process with three teeth found in the former species but not in the latter (Figs. 12, 17). The distal arm of the paracymbium of *N. trifididens* (Fig. 14) is wider than that of *N. sanctaehelenae* (Fig. 1). See diagnosis under *Napometa sanctaehelenae* for more details.

Description.—*Male* (High Central Ridge): Cephalothorax is illustrated in Figs. 16, 17. Measurements and a detailed description of the somatic morphology are provided by Benoit (1977). Total length 4.85. Cephalothorax 2.50 long, 1.90 wide; abdomen 2.25 long,
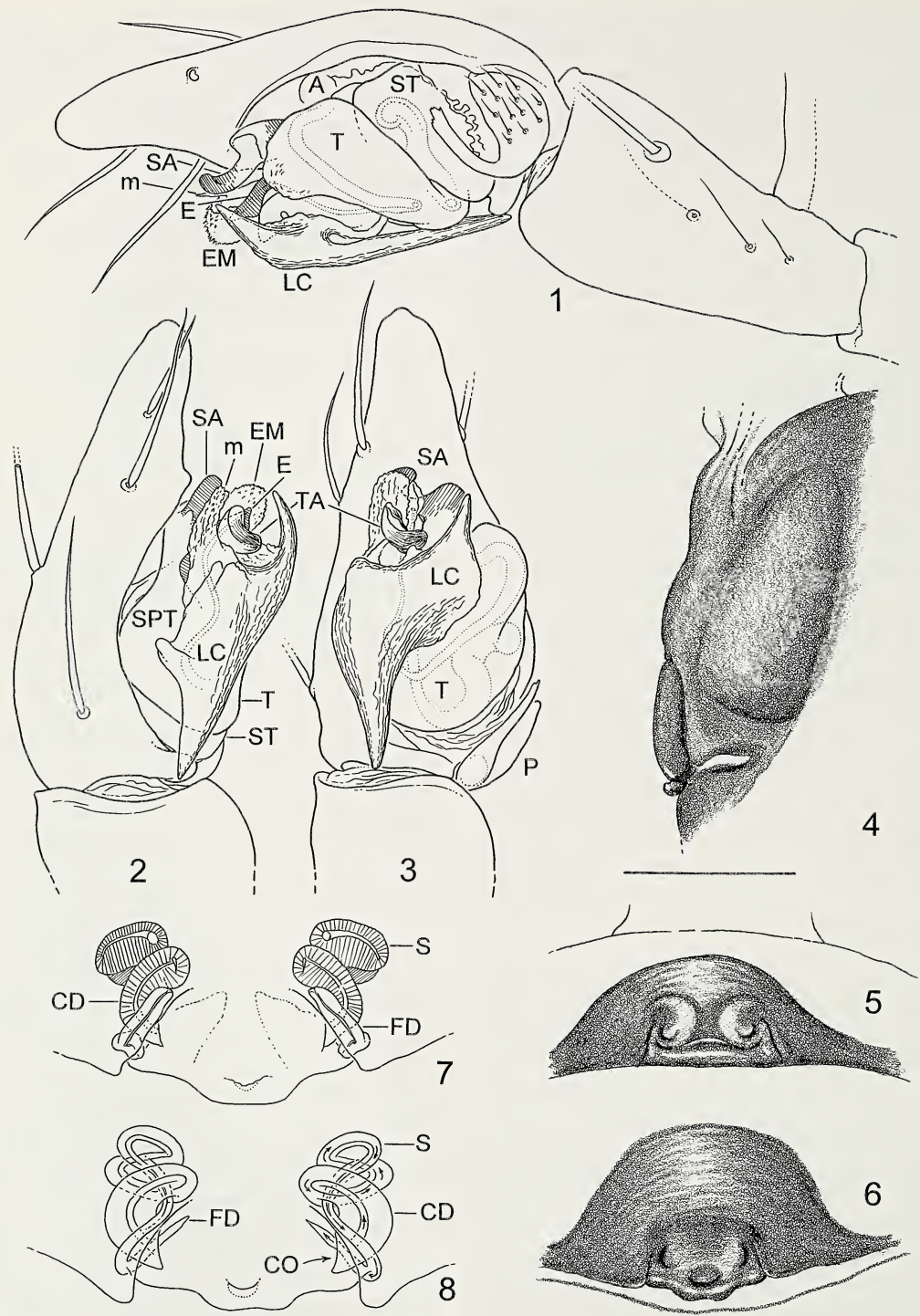
Figures 1–8.—*Napometa sanctaehelenae* Benoit. 1–3, Left male palpus (paratype); 1, Ectal (broken trichobothria are indicated by dotted lines); 2, Mesal; 3, Ventral. 4–8, Epigynum (paratype); 4, Lateral; 5, Caudal; 6, 7, Ventral; 8, Schematic, ventral. (Scale bar = 0.5 mm).'
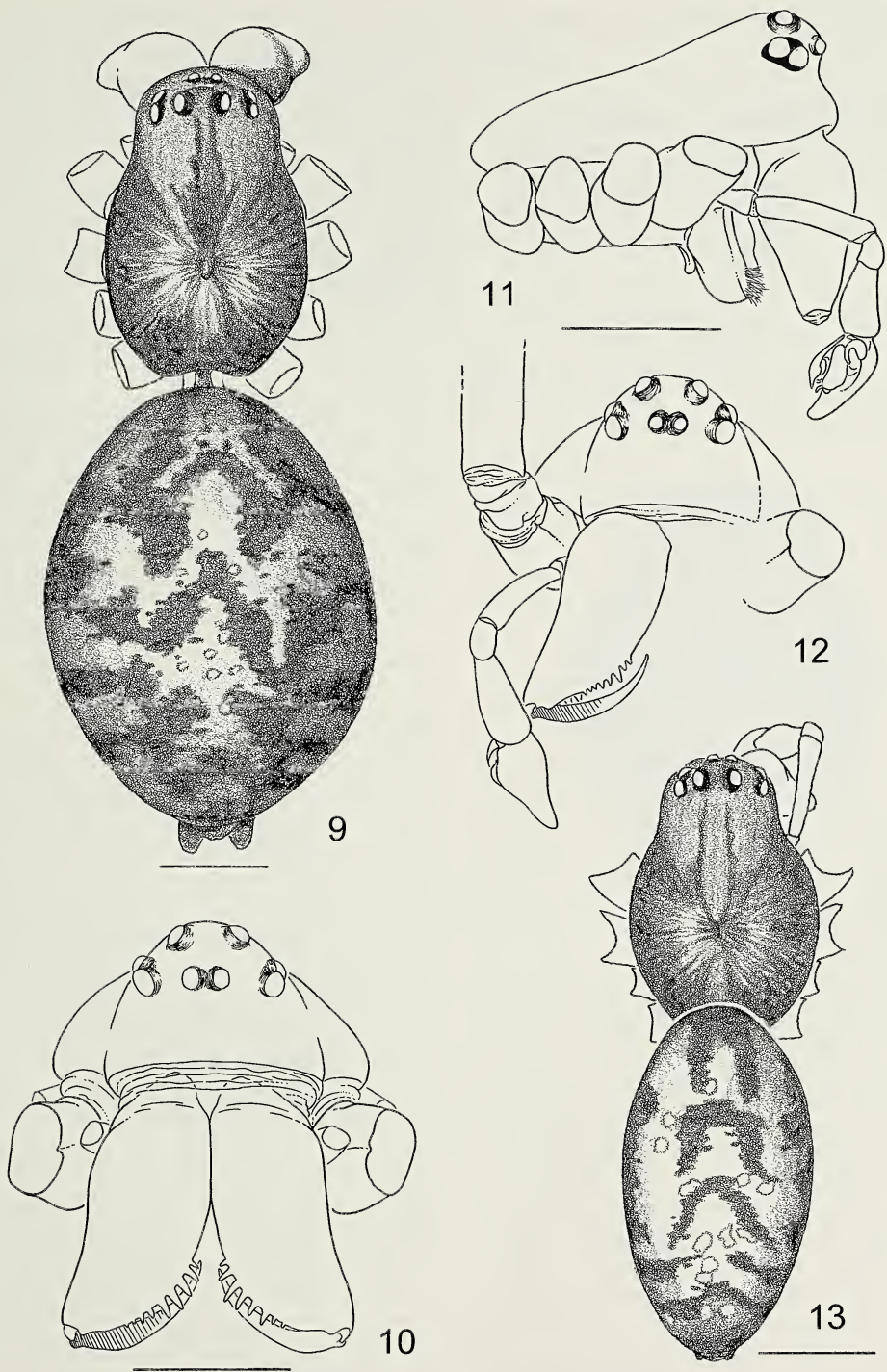
Figures 9–13.—*Napometa sanctaehelenae* Benoit. 9, Female paratype, dorsal view; 10, Female paratype, anterior view; 11, Male paratype, lateral view; 12, Male paratype, anterior view (left chelicera removed); 13, Male paratype, dorsal view. (Scale bars = 1.0 mm).
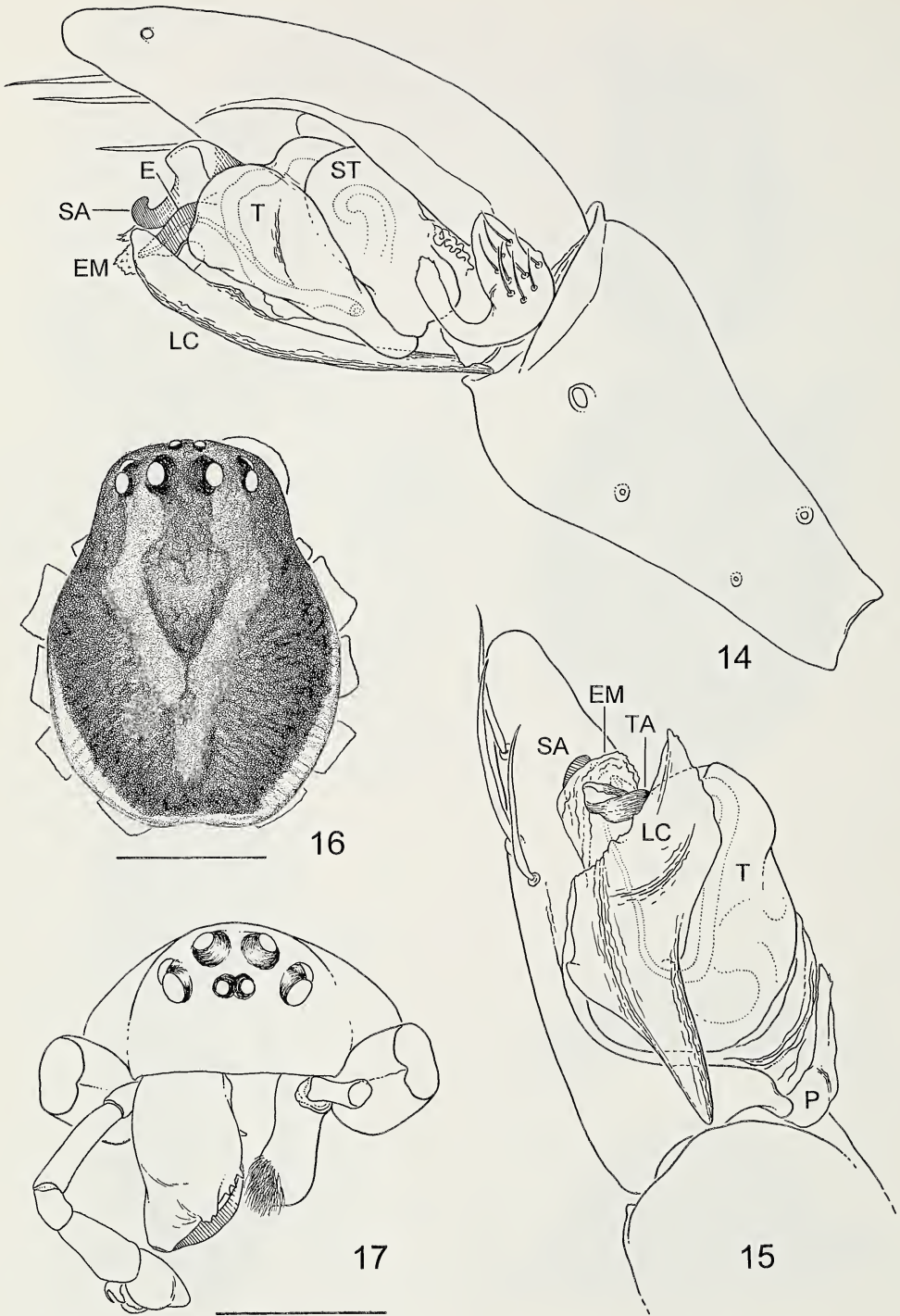
Figures 14–17.—*Napometa trifididens* (O. Pickard-Cambridge), male from Ste. Hélène Centre, High Central Ridge. 14, Palp, ectal; 15, Palp, ventral; 16, Cephalothorax, dorsal view (left chelicera removed); 17, Cephalothorax, anterior view. (Scale bars = 1.0 mm).

1.50 wide. Chelicerae with 5–6 prolateral (3 are grouped on an anteromesal process, Fig. 17) and 5 retrolateral teeth. Palp (Figs. 14, 15): Tibia almost as long (*ca.* 80%) as the cymbium; one prolateral and two retrolateral trichobothria. Cymbium with one ectal, three mesal and one dorsal macrosetae. Lamella with a flat and relatively wide ectodistal process, a rounded projection on the mesodorsal margin, and a long and pointed posterior process.

Distribution.—Known only from St. Helena island.

Material examined.—Male from St. Helena, labels state "Napometa trifididens ♂ O.P.C.; DET. P.L.G. Benoit 1970; LOC. Ste. Hélène Centre: High Central Ridge 2600/2700 ft. 17/XII/1965; REC. P. Basilewsky, P. Benoit, N. Leleup; R.G. Mus. Afr. Centr. 133.778," "Mission Zoologique Belge 1965/66 (P. Basilewsky, P. Benoit, N. Leleup)" and "MT 133.778." Deposited at the Royal Museum for Central Africa (Tervuren).

DISCUSSION

Napometa sanctaehelenae and *N. trifididens* lack two of the three known synapomorphies of Tetragnathidae (Hormiga et al. 1995), namely the conductor and the embolus spiraling with each other and the tegular sclerites in apical position. These two species share with tetragnathids and linyphiids the absence of the araneoid median apophysis. On the other hand *Napometa* species have three out of the four synapomorphies of linyphioids (Pimoidae plus Linyphiidae; Hormiga 1993, 1994a, b): absence of paracymbial apophyses, autospasy at the patella-tibia junction, and enlargement of the peripheral cylindrical silk gland spigot base on the PLS. In addition *Napometa* has the following linyphiid synapomorphies (Hormiga 1994b, 1995): intersegmental paracymbium, suprategulum, absence of median apophysis and conductor, embolic membrane, radix, and column (the latter two characters require confirmation by dissecting the embolic division when more specimens become available for study). Therefore, *Napometa* species are members of the Linyphiidae, not of the Metinae, as Benoit (1977) had suggested when he described the genus. Ironically, *N. trifididens* had been correctly described as a linyphiid by O. Pickard-Cambridge (1873), although this author thought

that *trifididens* could be a close relative of the metines:

> "*L. (Linyphia) trifididens* shows a decided approach to Spiders of the genera *Pachygnatha* and *Meta*; and it is not without some hesitation that I have (in absence of any knowledge of its habits) placed it in the genus *Linyphia*" (*op. cit.*, p. 222).

Simon (1894) transferred *trifididens* to the theridiid genus *Enoplognatha* (although he expressed some doubts about its affinities), perhaps because the large chelicerae of *trifididens* had some resemblance to those of *Enoplognatha*.

Benoit mistakenly thought of these two linyphiid species as metines, perhaps based on some notion of overall somatic similarity (although this is not explicitly stated in his text). Benoit's diagnosis of *Napometa* focuses almost exclusively on somatic characters (with the exception of the cymbium shape) and is written in the context of how to tell the genus apart from *Meta* (Tetragnathidae). Nevertheless, much of the cladistic evidence at the higher level in tetragnathids and linyphiids comes from the male palpal morphology (e.g., Hormiga 1994b; Hormiga *et al.* 1995). The lack of cladistic hypotheses in linyphiid systematics (see Hormiga 1994b) makes it impossible at the present time to hypothesize, on the basis of shared apomorphies, what the closest relatives of *Napometa* may be. It also prevents any attempts to provide a phylogenetic characterization (i.e., based on synapomorphies) of the genus. Nevertheless, the genitalic morphology of *Napometa* suggests that its close relatives may be found in the linyphiid clade that includes the genera *Neriene* Blackwall 1833, *Linyphia* Latreille 1804 and *Microlinyphia* Gerhardt 1928 (van Helsdingen 1969, 1970), although *Napometa* does not fit in any of these three genera as they are currently defined. Understanding the origin and phylogenetic position of *Napometa* therefore will not be possible until we have a cladistic hypothesis for the higher level systematics of linyphiids.

ACKNOWLEDGMENTS

LITERATURE CITED

Benoit, P.L.G. 1977. La faune terrestre de l'Sle de Sainte-Hélène, quatrième partie, 3. Arachnida: 3. Araneae, 22. Fam. Araneidae. Ann. Mus. Roy. Afrique Centrale (Zool.), 220:184–188.

Bonnet, P. 1956. Bibliographia Araneorum. Vol. 2, part 3, pp. 1927-3026. Toulouse: Les Frères Douladoure.

Brignoli, P.M. 1983. A Catalogue of the Araneae Described between 1940 and 1981. Manchester Univ. Press. Manchester, 755 pp.

Coddington, J.A. 1983. A temporary slide mount allowing precise manipulation of small structures. Pp. 291–292, *In* Taxonomy, Biology, and Ecology of Araneae and Myriapoda. (O. Kraus, ed.). Verh. Naturwiss. Ver. Hamburg, New Series 26.

Dippenaar-Schoeman, A.S. & R. Jocqué. 1997. African Spiders. An Identification Manual. Plant Protection Research Institute Handbook No. 9. Pretoria. 392 pp.

Holm, C. 1979. A taxonomic study of European and East African species of the genera *Pelecopsis* and *Trichopterna* (Araneae, Linyphiidae), with descriptions of a new genus and two new species of *Pelecopsis* from Kenya. Zool. Scripta, 8:255–278.

Hormiga, G. 1993. Implications of the phylogeny of Pimoidae (new rank) for the systematics of linyphiid spiders (Araneae, Araneoidea, Linyphiidae). Mem. Queensland Mus., 33:533–542.

Hormiga, G. 1994a. A revision and cladistic analysis of the spider family Pimoidae (Araneoidea, Araneae). Smithsonian Contrib. Zool. 549:1–104.

Hormiga, G. 1994b. Cladistics and the comparative morphology of linyphiid spiders and their relatives (Araneae, Araneoidea, Linyphiidae). Zool. J. Linnean Soc., 111:1–71.

Hormiga, G., W.G. Eberhard & J.A. Coddington. 1995. Web construction behavior in Australian *Phonognatha* and the phylogeny of nephiline and tetragnathid spiders (Araneae, Tetragnathidae). Australian J. Zool., 43:313–364.

Melliss, J.C. 1875. St. Helena: A Physical, Historical and Topographical Description of the Island. London, 425 pp.

Pickard-Cambridge, O. 1873. On the spiders of St. Helena. Proc. Zool. Soc. London, 1873:210–227.

Platnick, N.I. 1989. Advances in Spider Taxonomy: A Supplement to Brignoli's "A Catalogue of the Araneae Described between 1940 and 1981." Manchester Univ. Press. Manchester, 673 pp.

Platnick, N.I. 1993. Advances in Spider Taxonomy 1988–1991. New York Entomol. Soc. & American Mus. Nat. Hist., New York, 846 pp.

Roewer, C.F. 1942. Katalog der Araneae von 1758 bis 1940. Vol. 1. Natura. Bremen, 1040 pp.

Simon, E. 1883. Études Arachnologiques. 14e Mémoire. XXI. Materiaux por servir á la Faune arachnologique des ;îles de l'Océan Atlantique. Ann. Soc. Entomol. France, (6)3:259–314.

Simon, E. 1894. Histoire naturelle des Araignées. Librairie Encyclopédique de Roret, Paris.

Van Helsdingen, P.J. 1969. A reclassification of the species of *Linyphia* Latreille, based on the functioning of the genitalia (Araneida, Linyphiidae) I. Zool. Verh. (Leiden), 105:1–303.

Van Helsdingen, P.J. 1970. A reclassification of the species of *Linyphia* Latreille, based on the functioning of the genitalia (Araneida, Linyphiidae) II. Zool. Verh. (Leiden), 111:1–86.

CUPIENNIUS REMEDIUS NEW SPECIES (ARANEAE, CTENIDAE), AND A KEY FOR THE GENUS

Friedrich G. Barth[1] and **Detlev Cordes**: Biozentrum, Institut für Zoologie, Universität Wien, Althanstr. 14, A-1090 Wien, Austria

ABSTRACT. A new representative of the neotropical genus *Cupiennius* Simon 1891 (Araneae, Ctenidae) was found in the highlands of central Guatemala. *Cupiennius remedius* new species is the ninth species established for the genus. Like all other species of *Cupiennius*, *C. remedius* is a hunting spider living in close association with monocotyledonous plants where it hides in a retreat during the day and is active at night. *C. remedius* is of medium size (carapace length *ca.* 8 mm) compared to the other species of the genus and is the only *Cupiennius* species known to live sympatrically with *C. salei*. Live animals show a spotted coloration pattern unusual for the genus. The distinctive features of the male bulbi and female epigyna are described and an example is given of the species-specific courtship vibrations. In addition, we provide a revised key for the genus *Cupiennius*.

RESUMEN. Hemos encontrado un nuevo representante del género neotropical *Cupiennius* Simon 1891 (Araneae, Ctenidae) en las regiónes montañosas del centro de Guatemala. *Cupiennius remedius* nueva especie es la novena especie establecida para el género. Como todas las otras especies de *Cupiennius*, *C. remedius* es una araña cazadora que vive en estrecha asociación con plantas monocotiledóneas, en las que se oculta durante el día en un refugio y es activa durante la noche. En comparación con las otras especies del género, *C. remedius* es de tamaño intermedio (alrededor de 8 mm de longitud del caparazón) y es la única especie de *Cupiennius* que se sabe que vive en simpatría con *C. salei*. Los animales vivos presentan un patrón de coloración manchado que no es habitual en el género. Describimos las características distintivas de los bulbos de los machos y de los epiginos de las hembras e incluimos un ejemplo de las vibraciones de cortejo específicas de la especie. Además, incluimos una clave revisada del género *Cupiennius*.

When we first revised the genus *Cupiennius* Simon 1891 (Lachmuth et al. 1984) the genus contained 21 nominal species. Seven species from Central America (including northern Columbia, Cuba, Haiti, and Jamaica) were recognized by the structure of their genital organs. Six of the seven species (the exception being *C. granadensis* (Keyserling 1877)) have been bred successfully in the laboratory.

Among the species excluded from the genus in our previous revision was *C. celerrimus* Simon 1891. The main reason for the exclusion was the lack of a holotype, the locality in Brazil which appeared unlikely for the genus, and the fact that *C. celerrimus* had not been found since 1891. However, Brescovit & von Eickstedt (1995) recently redescribed *C. celerrimus* from Brazil; and we have therefore included it in our revised key as the ninth species of the genus *Cupiennius*.

A particular incentive for the clarification of the taxonomy of *Cupiennius* is the importance of some of its representatives in studies in sensory and behavioral physiology (Barth 1985, 1993; Barth et al. 1993a,b, 1995; Humphrey et al. 1993; Lachmuth et al. 1984; Land & Barth 1992; Strausfeld & Barth 1993). An extensive study of problems in reproductive isolation of the species (Barth 1993) also prompted a PCR-analysis of DNA-sequences which provided evidence for the polyphyly of the family Ctenidae to which the genus *Cupiennius* is assigned (Huber et al. 1993).

Cupiennius remedius new species was found in 1992 while searching for *C. salei* (Keyserling 1877) in the highlands of central Guatemala at the Finca Remedios (Fig. 1). *C. remedius* is the only species of the genus known to live sympatrically with *C. salei*. The present study describes the new species and in addition provides a revised key for the genus. The key also considers some new aspects

[1]To whom correspondence should be addressed.
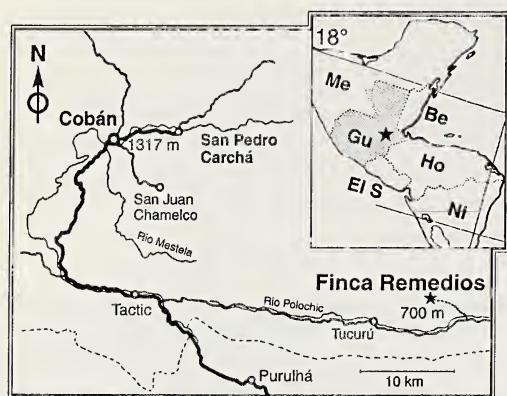
Figure 1.—The location of Finca Remedios in Guatemala (Alta Verapaz) where **Cupiennius remedius** new species was found.

which have emerged from many years of research in the field and in the laboratory as well as from breeding most of the species.

Cupiennius remedius new species
Figs. 1–5, 13

Types.—Male holotype, two male and four female paratypes were collected at the Finca Remedios on 12 February 1992 (F.G. Barth, R. Felber). One of the spiders was collected as a juvenile and developed into an adult male in the laboratory. The holotype and one female paratype are in the arachnological collection of the Senckenberg Museum, Frankfurt am Main, Germany. The other paratypes

remain in the collection of the Zoology Department of the University of Vienna, Austria.

Etymology.—The name of the new species refers to the type locality, i.e., Finca Remedios.

Diagnosis.—Morphologically, *C. remedius* forms a group together with *C. foliatus* F.P.-Cambridge 1901 and *C. panamensis* Lachmuth et al. 1984, of which it is the largest (Fig. 2). The spotted appearance of its habitus is unique among all known species of *Cupiennius* (Fig. 3). In addition, male *C. remedius* differ from male *C. foliatus* by the terminal apophysis of their bulbs which is not elevated at the embolic base (stipes-embolus) as it is in *C. foliatus* (Figs. 30, 31). Regarding the females, a prominent difference between *C. remedius* and *C. foliatus* is the shape of the lateral plates of the epigynum at their anterior end (Fig. 14a). Apart from the spotted habitus, the lateral plates of the epigynum also distinguish *C. remedius* from *C. panamensis*. In *C. remedius*, the lateral plates are not continuous with the median septum (Fig. 14a). Whereas the vulvae are strikingly similar in *C. remedius* and *C. foliatus* (Fig. 22), the shape of the seminal ducts leading to the seminal receptacles I clearly differs between *C. remedius* and *C. panamensis* (Figs. 21, 22). The strong twisting of the seminal ducts of the first receptacles in *C. remedius* and *C. foliatus* is very conspicuous but typical of *C. salei* as well (see Figs. 15, 22).
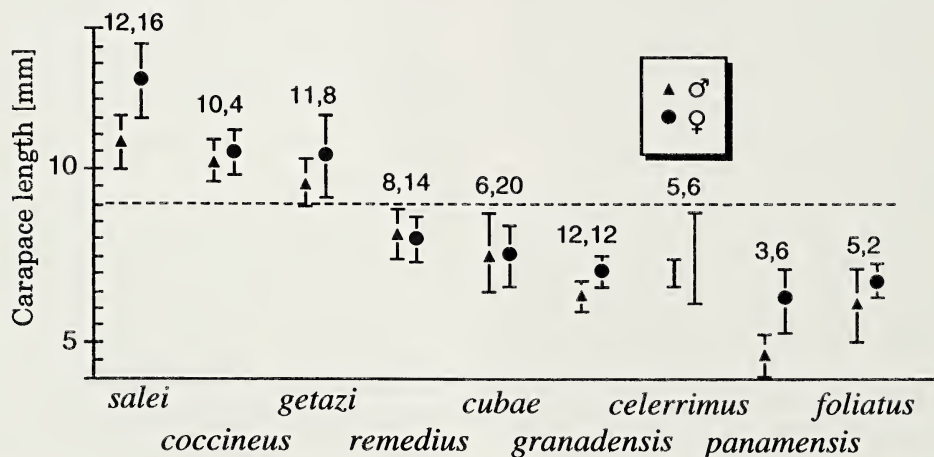
Figure 2.—Size distribution of the nine known species of *Cupiennius*, indicated by the carapace lengths of male and female representatives. Number of individuals measured is given above the symbols. Bars represent standard deviation of the mean; for *n* < 7 the bars instead represent the range of values. For *C. celerrimus* the range of values given is taken from Brescovit & Eickstedt 1995.
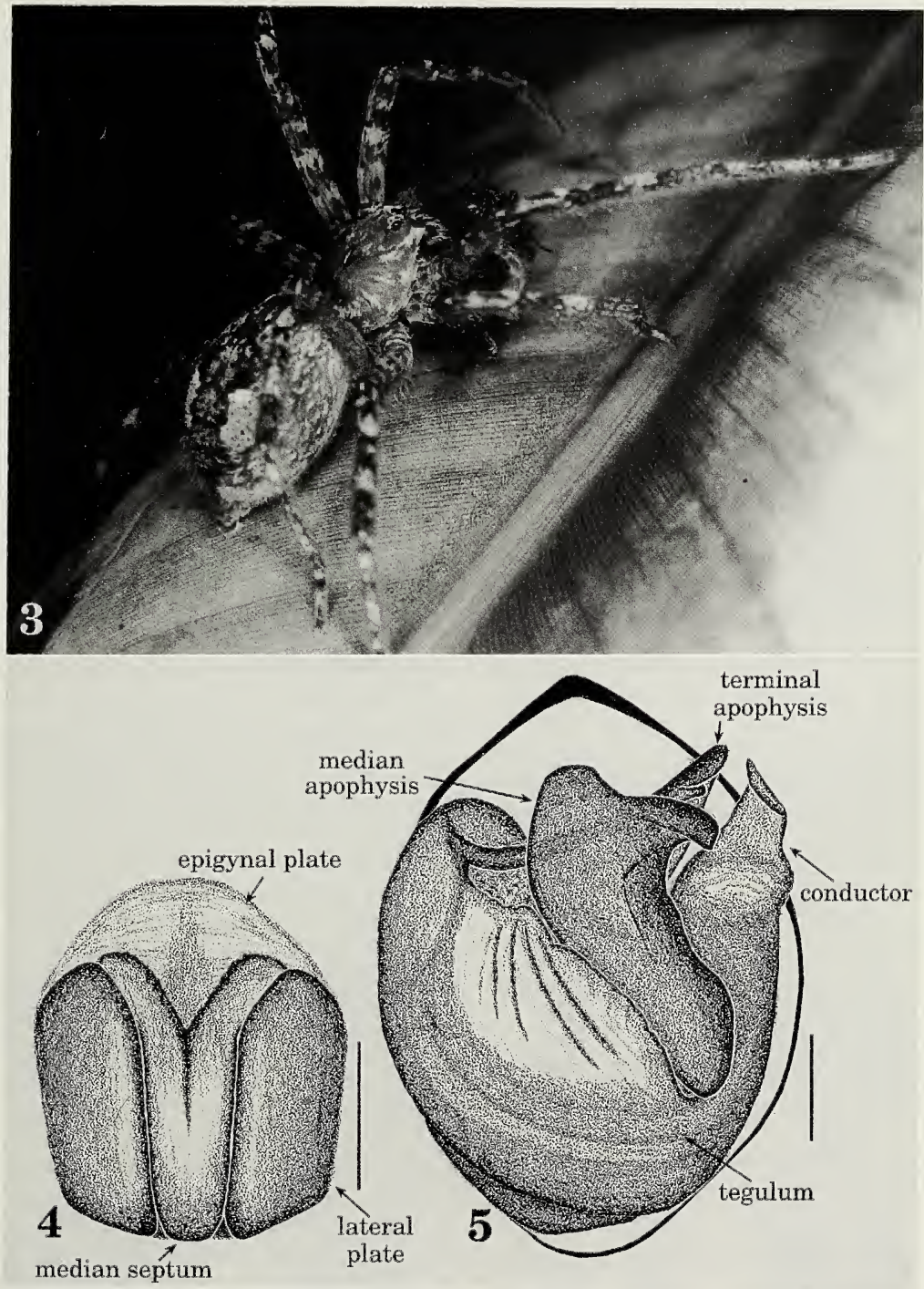
Figures 3–5.–*Cupiennius remedius* new species. 3, Adult female, feeding on a fly; 4, Epigynum of female paratype, ventral view; 5, Bulb and terminal parts of embolus of male holotype, ventral view. Scale = 0.5 mm.
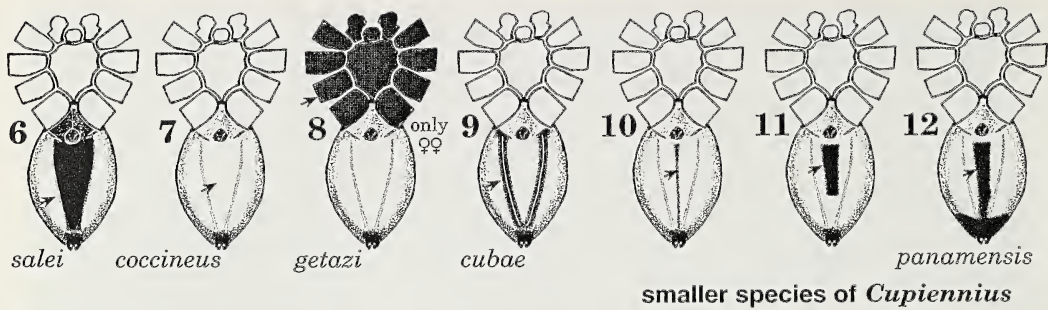
Figures 6–12.—Schematized view of the ventral body of different species of *Cupiennius* to show diversity of ornamental patterns (see arrows). 6, *C. salei*; 7, *C. coccineus*; 8, *C. getazi*; 9, *C. cubae*. 10–12. Smaller *Cupiennius* species, range of pattern variability (12, *C. panamensis*).

Description.—*Males:* Prosoma 7–9 mm long ($\bar{x}$ = 8.2 mm, Fig. 2), medium brown with a patchy pattern dorsally (Fig. 3). Opisthosoma dorsally medium brown with light brown markings along the cardiac mark; ventrally light with a slight brown indication of a narrow median stripe or with a distinct dark and narrow median stripe (Figs. 10, 11), variable. Legs light brown without ring-shaped patterns; femur clearly lighter than the other leg segments; tarsus, metatarsus, and tibia covered by conspicuous long thin hairs ventrally and laterally. Pedipalps medium brown with a short tibial apophysis typical of the genus. Bulb (Fig. 5) with its prominent median apophysis slightly curved with a round terminal and a large shovel-like lateral process; conductor largely flat and tip bent towards tegular apophysis; terminal elements (Fig. 30): embolic apophysis distinctly curved, terminal apophysis leaf-like and covering the embolic opening.

Females: Prosoma 7.4–9.3 mm long ($\bar{x}$ = 7.9 mm, Fig. 2), medium brown with a light brown, patchy pattern dorsally (Fig. 3). Opisthosoma dorsally medium brown with light brown markings along the cardiac mark; ventral side light with a dark narrow median stripe (Figs. 10, 11). Legs medium to light brown with distinct annular patterns (Fig. 3). Epigynum (Fig. 4) with narrow median septum slightly narrowing distally and dividing into two parts proximally (bordering the lateral plates), its Y-shape similar to that of *C. foliatus*; lateral plates elevating towards median septum and connecting to the border of the epigynal plate anterio-laterally; vulva with more or less ball-shaped first receptacles and seminal ducts strongly winding dorsally and proximally (Fig. 22).

Courtship behavior.—*Cupiennius remedius* is the seventh among all known species of the genus (together with *C. salei*, *C. getazi* Simon 1891, *C. coccineus* F.P.-Cambridge 1901, *C. cubae* Strand 1910, and *C. foliatus*) which has been shown to be a biospecies. We have bred *C. remedius* in Vienna and also observed its courtship behavior. As known from extensive studies with other species of *Cupiennius* (Barth & Schmitt 1991; Barth 1993), the vibrations exchanged between male and female during courtship are important in the reproductive isolation of the species; and it is in particular the male courtship vibration which helps the female to
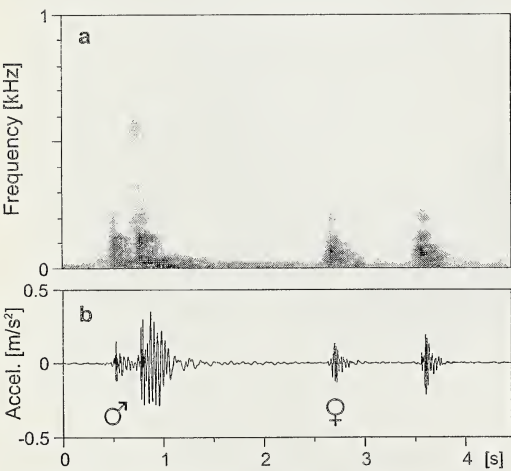
Figure 13.—Sonagram and oscillogram of representative substrate borne male courtship vibration and female vibratory response of *Cupiennius remedius* new species. Signals were recorded on a bromeliad using an accelerometer.
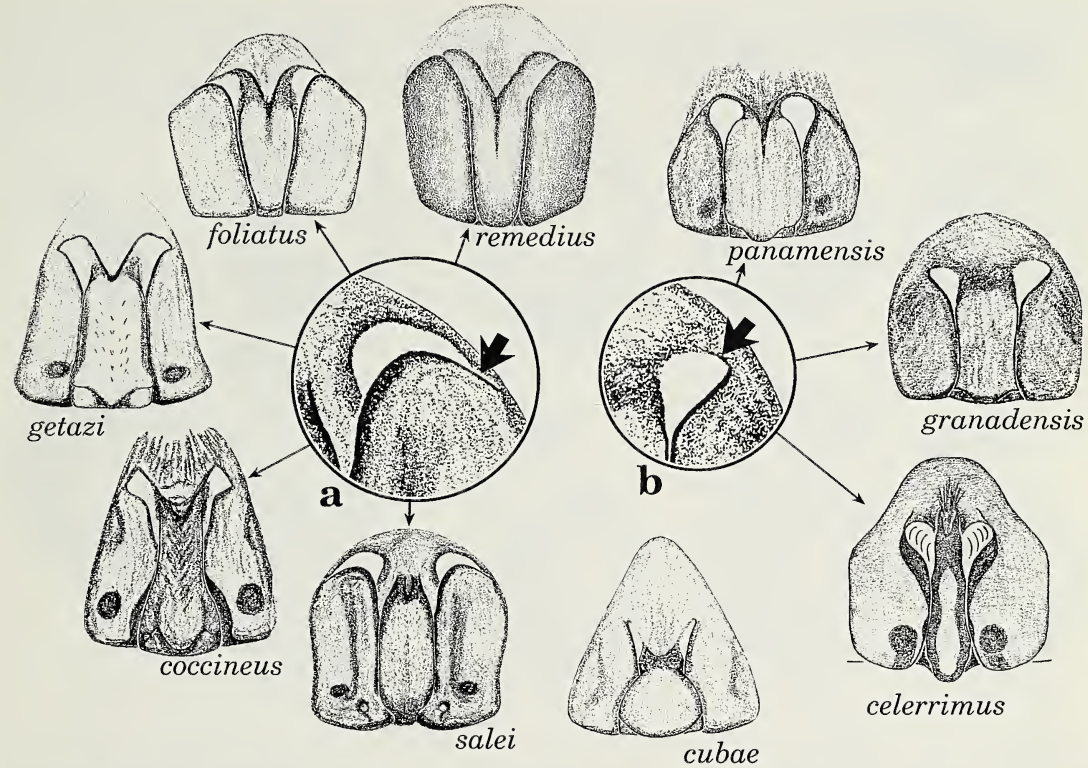
Figure 14.—Ventral view of epigyna of the females of all nine species of *Cupiennius*. Note two groups **a** and **b** which differ with regard to the way in which the lateral plates are connected to the epigynal plate anterio-laterally. See Fig. 3 for nomenclature of various parts. Modified and adapted from Lachmuth et al. 1984 and from Brescovit & von Eickstedt 1995 (*C. celerrimus*).
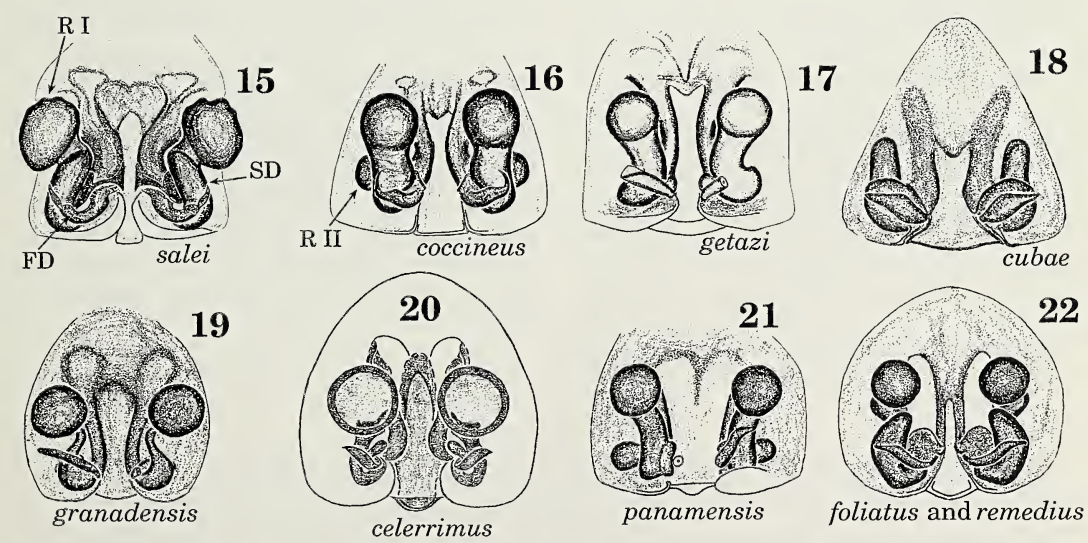
Figures 15–22.—Epigyna of the females of the nine *Cupiennius*-species. Seen in dorsal view (from inside) and showing the seminal receptacles I and II (RI, RII), the seminal duct (SD) and the fertilization duct (FD). Modified and adapted from Lachmuth et al. 1984 (Figs. 15–19, 21, 22) and Brescovit & von Eickstedt 1995 (Fig. 20).
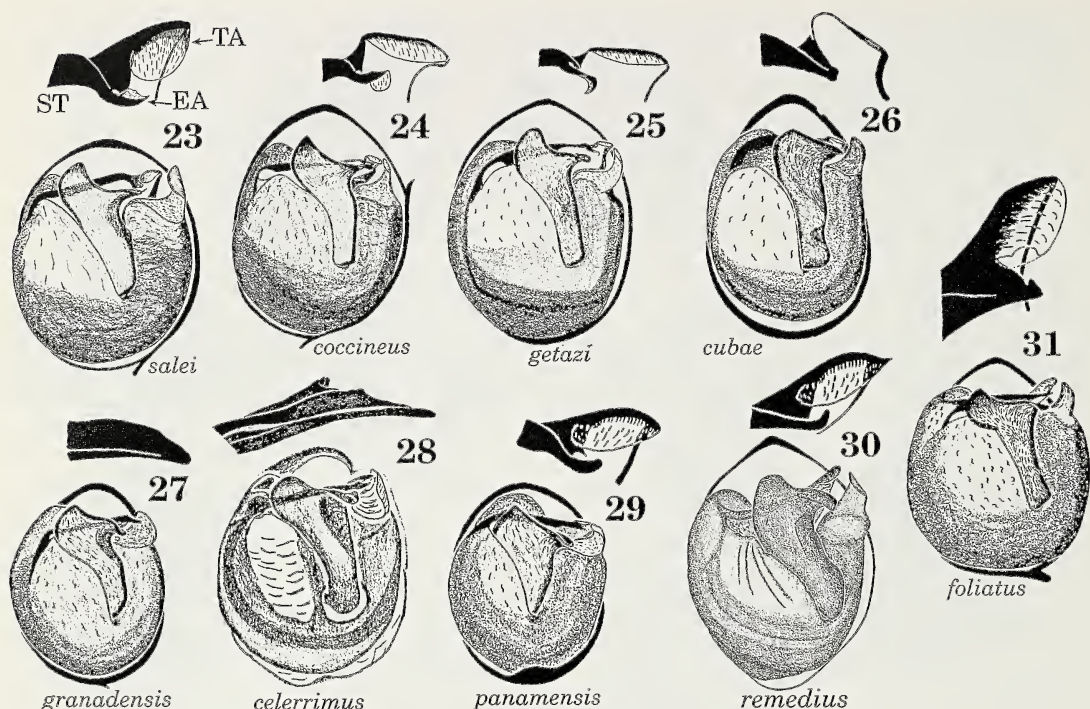
Figures 23–31.—Bulbi genitales and terminal parts of the embolus of the males of all nine species of *Cupiennius*. For the terminology of the various parts see Fig. 3; TA = terminal apophysis, SE = stipes embolus, EA = embolic apophysis. Modified and adapted from Lachmuth et al. 1984 (Figs. 23–27, 29, 31) and from Brescovit & von Eickstedt 1995 (Fig. 28).

recognize its conspecific partner. In *C. remedius* the male vibration results from up and down movements of the opisthosoma (without touching the substrate; Dierkes & Barth 1995) and does not come in series of syllables as in *C. coccineus, C. getazi,* and *C. salei* (Barth 1993). Instead it is a single syllable resulting from a short bang of the pedipalps onto the dwelling plant followed by just one or two cycles of the opisthosomal movement (Fig. 13). The main frequency components are around 30 Hz in case of both the male vibration and the female response.

Distribution.—Until now, *C. remedius* was

known only from the type locality. The Finca Remedios is located in the Departamento Alta Verapaz near Coban at an altitude of about 700 m (Fig. 1) and with the climate typical of the "tierra templada" (Barth & Seyfarth 1979; Barth et al. 1988). All animals were collected at the edge of a banana plantation 4 km east of the finca house and close to a small brook and an unpaved road. The spiders all sat behind the trough-shaped basal parts of banana leaf sheaths which are typical retreats of other species of *Cupiennius* as well (Barth et al. 1988).

KEY TO THE SPECIES

The following key includes the description of the coloration patterns, typical of living representatives of the species. In the larger species, this permits determination of the species even for subadult specimens. The coloration may be indistinct or even absent in preserved specimens. Then the shape of the epigynum, vulva and bulbal sclerites is of major importance. Especially the smaller species of *Cupiennius* have an indistinct or variable coloration pattern on their body and legs. Their determination is possible only by dissecting the vulva (females) or looking at small details of the male bulb. The key includes all important features of the genitalia already described in Lachmuth

et al. (1984). Besides including *C. remedius* and *C. celerrimus*, it extends the previously published key by considering body size and additional characters of the coloration pattern and of the genitalia. The definition of the colors used in the key is taken from a color table of color-pencils from Faber-Castell, Germany.

Adult Females:

1. Large spider (carapace length > 9 mm) (Fig. 2); legs and/or body with conspicuous markings or color pattern 2
    Medium sized spider (carapace length < 9 mm) (Fig. 2); legs and/or body uniformly brown or with comparatively indistinct or variable markings 4
2.(1) Legs brown with conspicuous dark markings 3
    Femora I–IV bright carmine-red ventrally; prosoma and opisthosoma medium to dark brown dorsally with a darker median band; ventral opisthosoma without any dark markings (Fig. 7); epigynum with narrow median septum, widening distally; distal part of septum with strongly sclerotized hook (Fig. 14a) .... *coccineus*
3.(2) Femora I–IV with distinct black annular patterns; prosoma dorsolaterally with light grayish-brown pattern contrasting the darker median band; coxae densely covered with terra cotta red hairs ventrally; ventral opisthosoma always with broad black median stripe (Fig. 6); in some specimens pairs of yellowish to whitish spots disto-laterally on both sides of the cardiac mark; epigynum with narrow median septum of uniform width (Fig. 14a); body length up to 45 mm (largest species, Fig. 2) .... *salei*
    Femora I–IV on the ventral side with many small black spots; either sternum or sternum and coxae (variable) dark brown to black (Fig. 8); dorsally, body coloration distinct and species-specific: median dark band on prosoma, colored areas laterally on the body; dark cardiac mark (opisthosoma); dark inverse V-shaped stripes, distal to cardiac mark; ventral opisthosoma light brown (populations from Barro Colorado Islands and from Panama were observed to have only a dark median ventral opisthosomal band, and no speckled femora). A grayish morph and an orange morph exist. Epigynum with broad median septum of roughly uniform width, but widening distally (Fig. 14a); distal part of septum with sclerotized nose-like process .... *getazi*
4.(1) Epigynal plate oval or trapezoid 5
    Epigynal plate distinctly triangular (Fig. 14b); median septum of epigynum strongly widened distally forming a sphere; seminal receptacle I cone-like; body color in general uniformly grayish to brownish, ventral opisthosoma with outlines of a dark median band, consisting of a series of short dark reddish hairs (Fig. 9) .... *cubae*
5.(4) Lateral plate of epigynum directly connected to the median septum forming a loop (Fig. 14b) 6
    Lateral plate of epigynum not directly connected to the median septum and extending to the anterior-lateral border of the epigynal plate (Fig. 14a) 8
6.(5) Epigynum with narrow median septum, seminal receptacles I with seminal ducts of different shapes: S-shaped, twisted, winding or rolled 7
    Epigynum wider than long (Fig. 14b); median septum broad and leaf-like; vulva: seminal receptacles I ball-shaped with seminal ducts sturdy and slightly curved laterally (Fig. 21); prosoma light brown; opisthosoma darker brown, with narrow dark-shaded median band ventrally (Fig. 11); smallest species (Fig. 2) .... *panamensis*
7.(6) Median septum with parallel borders, distally ending broad, and with a small hook (Fig. 14b); vulva: seminal receptacles I with distinctly S-shaped seminal ducts (Fig. 19) .... *granadensis*
    Median septum long, narrow and slightly widening distally (Fig. 14b); vulva: seminal receptacles large and ball-shaped, seminal ducts rolled dorso-ventrally (Fig. 20); body orange to brown with darker brown median band, legs I–IV yellow ventrally on coxae and femora .... *celerrimus*
8.(5) Lateral plates of epigynum ending rounded before connecting to the epigynal plate (Fig. 14a), median septum of epigynum narrow and continuously narrowing distally (Fig. 14a); vulva with ball-shaped seminal receptacles, seminal ducts strongly winding (Fig. 22); medium large spider (carapace length 7–8 mm); annular patterns on femora, and body remarkably spotted (Fig. 3); tarsi of legs I–IV with long dark hairs both dorsally and ventrally .... ***remedius*** new species
    Lateral plates of epigynum ending as indicated in Fig. 14a before connecting to the anterior-lateral end of the epigynal plate, median septum of epigynum as in Fig. 14a; seminal receptacles I ball-shaped, seminal ducts as in Fig. 22; spider smaller (carapace length up to 7 mm); body

without distinct color pattern or with a series of dark spots along the cardiac mark on the opisthosoma .... *foliatus*

Adult Males:

1. Large spider (carapace length > 9 mm) (Fig. 2). Legs with conspicuous markings (except one case, see 2.); body light gray, light brown to medium brown or bright orange dorsally; ventral opisthosoma with or without broad dark median stripe 2

   Medium sized spider (carapace length < 9 mm) (Fig. 2). Legs and/or body uniformly brown or with indistinct markings, or pro- and opisthosoma with variable arrangement of more or less isolated dark dots and lines; opisthosoma light ventrally or with a narrow dark median stripe
   4

2.(1) Legs and/or body with conspicuous markings 3

   Legs without conspicuous coloration; legs and body gray-brown with median band on dorsal prosoma consisting of thin dark lines; light opisthosoma with dark cardiac mark, lacking dark markings ventrally; bulb with terminal apophysis bent downwards, embolic-apophysis strongly curved and twisted (Fig. 24) .... *coccineus*

3.(2) Femora I–IV with distinct black annular patterns ventrally; body grayish dorsally with dark lines along the length of the prosoma (= median band); sternum and coxae grayish; opisthosoma with broad dark median band ventrally; bulb with terminal apophysis large and bent downwards, embolic apophysis robust and curved (Fig. 23); body length up to 30 mm (largest species, Fig. 2) .... *salei*

   Femora I–IV with many small black spots ventrally; sternum and coxae dark brownish (variable); conspicuous species-specific body coloration: a dark median band dorsally on prosoma and opisthosoma bordered by light areas laterally; dark cardiac mark dorsally on opisthosoma, and dark inverse V-shaped stripes posterior to it; two morphs with either grayish or orange basic coloration. Bulb with terminal apophysis bent downwards, embolic apophysis strongly curved and twisted (Fig. 25) .... *getazi*

4.(1) Opisthosoma with narrow dark median stripe ventrally (Figs. 10–12) or without ventral markings 5

   Opisthosoma only with dark reddish outlines of the ventral median stripe (Fig. 9); bulb (Fig. 26) with median apophysis comparatively straight and notched in the proximal third of its length, distal process and lateral shovel-like process very small, terminal apophysis strongly domed and extending over the short embolic apophysis. Body grayish or brownish ......*cubae*

5.(4) Bulb with embolic base (stipes-embolus) massive (Figs. 27, 28), terminal and embolic apophysis not distinct 6

   Embolic base (stipes-embolus) with distinct terminal and embolic apophysis (Figs. 23–26, 29–31) 7

6.(5) Embolic base (stipes-embolus) bill-shaped and folded forming one furrow (Fig. 27); body light yellow-brown with a sparse coverage of hairs; prosoma with median line markings dorsally
   .... *granadensis*

   Embolic base (stipes-embolus) strongly folded forming two furrows (Fig. 28); embolic tip appears severed with a pair of short processes; body and legs orange with a brown median band on pro- and opisthosoma; ventral surface of coxae and femora yellow ...... *celerrimus*

7.(5) Terminal apophysis levels with the embolic base (stipes-embolus) (Figs. 29, 30) 8

   Terminal apophysis elevates at an angle of approximately 45° at the embolic base (Fig. 31) and covers the embolic apophysis; opisthosoma with a variable line of spots along the border of the cardiac mark .... *foliatus*

8.(6) Carapace length *ca.* 8 mm; body with spotted coloration pattern dorsally; legs long (sexual-dimorphic), covered with a "brush" of long and thin hairs along the tibia and metatarsus and with the longest hairs at the proximal part of the tibia-metatarsus joint; median apophysis with an elevation near the lateral process, tegulum with deep furrows ventrally (Fig. 5) .... *remedius* new species

   Carapace length *ca.* 5 mm; body without distinct coloration pattern dorsally; dorsal opisthosoma darker than prosoma and with a small dark median band ventrally, widening towards the posterior part of the opisthosoma (Fig.12) .... *panamensis*

LITERATURE CITED

Barth, F.G.(ed.). 1985. Neurobiology of Arachnids. Springer-Verlag, Berlin.

Barth, F.G. 1993. Sensory guidance in spider precopulatory behavior. Comp. Biochem. Physiol., 104A:717–733.

Barth, F.G. & A. Schmitt. 1991. Species recognition and species isolation in wandering spiders (*Cupiennius* spp., Ctenidae). Behav. Ecol. Sociobiol., 29:333–339.

Barth, F.G., J.A.C. Humphrey, U. Wastl, J. Halbritter & W. Brittinger. 1995. Dynamics of arthropod filiform hairs. III. Flow patterns related to air movement detection in a spider (*Cupiennius salei* Keys.). Phil. Trans. R. Soc. London, B, 347:397–412.

Barth, F.G., T. Nakagawa & E. Eguchi. 1993a. Vision in the ctenid spider *Cupiennius salei*: spectral range and absolute sensitivity (ERG). J. Exp. Biol., 181:63–79.

Barth, F.G., U. Wastl, J.A.C. Humphrey & R. Devarakonda. 1993b. Dynamics of arthropod filiform hairs. II. Mechanical properties of spider trichobothria (*Cupiennius salei* Keys.). Phil. Trans. R. Soc. London, B, 340:445–461.

Barth, F.G. & E.-A. Seyfarth. 1979. *Cupiennius salei* Keys. (Araneae) in the highlands of central Guatemala. J. Arachnol., 7:255–263.

Barth, F.G., E.-A. Seyfarth, H. Bleckmann & W. Schüch. 1988. Spiders of the genus *Cupiennius* Simon 1891 (Araneae, Ctenidae). I. Range distribution, dwelling plants, and climatic characteristics of the habitats. Oecologia, 77:187–193.

Brescovit, A.D. & V.R.D. von Eickstedt. 1995. Ocorrência de *Cupiennius* Simon na América do Sul e redescriçâo de *Cupiennius celerrimus* Simon (Araneae, Ctenidae). Rev. Brasiliera Zool., 12(3):641–646.

Dierkes, S. & F.G. Barth. 1995. Mechanism of signal production in the vibratory communication of the wandering spider *Cupiennius getazi* (Arachnida, Araneae). J. Comp. Physiol. A, 176:31–44.

Huber, K.C., T.H.S. Haider, M.W. Müller, B.A. Huber, R.J. Schweyen & F.G. Barth. 1993. DNA-sequence data indicates the polyphyly of the family Ctenidae (Araneae). J. Arachnol., 21:194–201.

Humphrey, J.A.C., R. Devarakonda, J. Iglesias & F.G. Barth. 1993. Dynamics of arthropod filiform hairs. I. Mathematical modelling of the hair and air motions. Phil. Trans. R. Soc. London, B, 340:423–444.

Keyserling, E. 1877. Über amerikanische Spinnenarten der Unterordnung Citigradae. Verh. Zool.-Bot. Ges. Wien, 26:609–708.

Lachmuth, U., M. Grasshoff & F.G. Barth. 1984. Taxonomische Revision der Gattung *Cupiennius* Simon 1891 (Arachnida; Araneae). Senckenbergiana Biol., 65:329–372.

Land, M.F. & F.G. Barth. 1992. The quality of vision in the ctenid spider *Cupiennius salei*. J. Exp. Biol., 164:227–242.

Pickard-Cambridge, F.O. 1897–1905. Biologia Centrali-Americana. Arachnida, Araneida and Opiliones, 2:1–610.

Simon, E. 1891. Description de quelques arachnides de Costa Rica communiqués par M.A. Getaz (de Genève). Bull. Soc. Zool. France, 16:109–112.

Strand, E. 1910. Eine neue cteniforme Spinne aus Guatemala. Soc. Entomol., 25:14.

Strausfeld, N.J. & F.G. Barth. 1993. Two visual systems in one brain: neuropils serving the secondary eyes of the spider *Cupiennius salei*. J. Comp. Neurol., 328:43–62.

THE NEST AND MALE OF THE TRAP-DOOR SPIDER
POECILOMIGAS BASILLEUPI
(ARANEAE, MYGALOMORPHAE, MIGIDAE)

Charles E. Griswold: Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118 USA

ABSTRACT. The male and nest of *Poecilomigas basilleupi* Benoit 1962 are described based on specimens from Tanzania. *Poecilomigas basilleupi* nests have a single door, differing in this regard from the two-door nests of *Poecilomigas abrahami* (O.P. Cambridge 1889). A revised key to *Poecilomigas* species is presented.

Poecilomigas are aptly referred to as tree trap-door spiders, building well-camouflaged trap-door nests on the trunks and buttresses of trees. This behavior was reported for the type species, *Poecilomigas abrahami* more than a century ago (O.P. Cambridge 1889). Recently I was able to observe similar behavior in the tropical African species of the genus. In this, the third in a series of papers on the Migidae of the Afrotropical region (Griswold 1987a, b), I describe the nest and hitherto unknown male of *Poecilomigas basilleupi* and confirm that the diagnosis of *Poecilomigas* suggested in Griswold (1987b) holds for both sexes of this species. A revised key to *Poecilomigas* species and discussion of variation in females of *P. basilleupi* are included.

The specimens were discovered and observations made at the Mazumbai Forest in the West Usambara Mountains of Tanzania. The Mazumbai Forest is located at 4°49′S, 38°30′E and ranges in elevation from 1300–1900 m. It comprises one of the best preserved remnants of lower montane evergreen and montane rainforest in east Africa (Redhead 1981; Scharff *et al.* 1996).

METHODS

The format of the description follows that in Griswold (1987a). Abbreviations are standard for the Araneae. All measurements are in millimeters. Eyes are measured from above. Due to difficulties in consistently locating the margins of the domed cuticular lens, the AME diameter is expressed as that of the shiny tapetum. The sternal sigilla are the concave regions near the sternal margin as viewed in

oblique lighting, not the discolored area associated with these structures. The three nests collected are deposited in the California Academy of Sciences (CAS).

TAXONOMY

Migidae Simon 1889

Diagnosis.—Distinguished from all other mygalomorphs by having the fang with dorsolateral keels (Fig. 9; Griswold 1987b: fig. 3), the ocular area at least 0.40× the width of the caput (Fig. 1), the thoracic fovea straight to recurved (Fig. 1), and lacking a rastellum on the chelicerae (Figs. 8, 9).

Genus *Poecilomigas* Simon

Poecilomigas Simon 1903: 23. Type species, by monotypy, *P. pulchripes* Simon (= *Moggridgea abrahami* O.P. Cambridge 1889). Roewer 1942: 192. Bonnet 1958: 3736. Brignoli 1983: 121. Griswold 1987b: 485. Platnick 1989: 73.

Diagnosis.—Distinguished from all migid genera except *Migas* L. Koch 1873 by having a tooth between the keels near the base of the fang (Fig. 9; Griswold 1987b: fig. 3), and from *Migas* by having dark dorsal and lateral maculations or annuli on the tibiae and metatarsi (Fig. 1).

Poecilomigas basilleupi Benoit

Poecilomigas basilleupi Benoit 1962: 276 (holotype, MRAC 112228, Mt. Kilimanjaro, Tanzania, examined). Brignoli 1983: 121. Griswold 1987b: 492. Platnick 1989: 73.

Diagnosis.—Distinguished from other *Poecilomigas* by having the dorsum and sides of
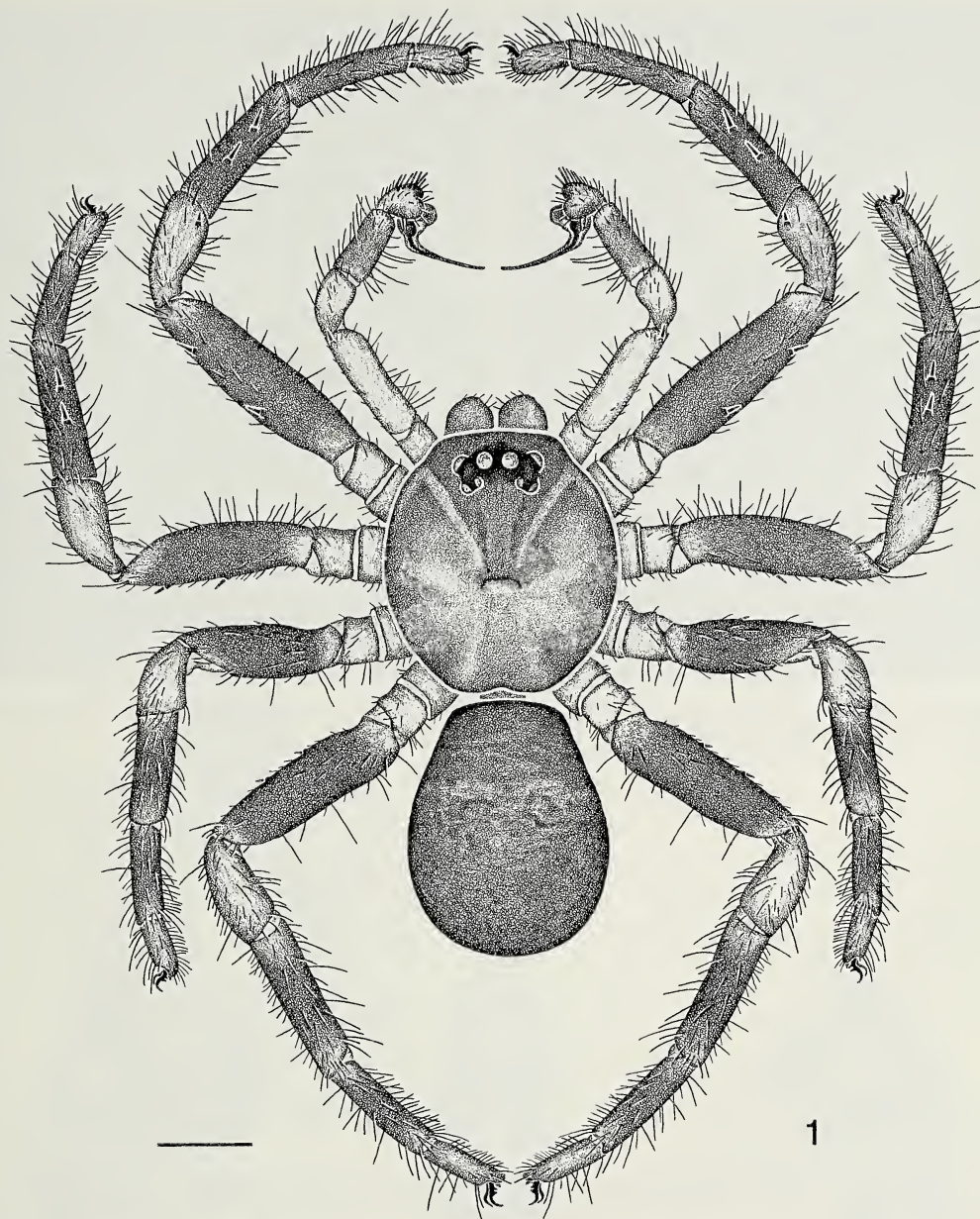
Figure 1.—Male of *Poecilomigas basilleupi,* Mazumbai, dorsal. Scale = 1.0 mm.

the abdomen entirely dark (Figs. 1, 8; Griswold 1987b: figs. 1, 33).

Description.—*Male:* (Mazumbai). Total length 6.53. Carapace orange-brown, becoming dusky at margins above coxae and on pair of faint longitudinal bands on caput (Fig. 1); ocular area black with black extending on clypeus half way to anterior margin; chelicerae yellow-brown; sternum, coxae, and tro-

chanters yellow- white; legs with dusky annuli extending over most of femora, tibiae, and metatarsi, leaving only patellae, tarsi, and regions near joints yellow-brown; pedipalpi yellow-white except for dusky annulus on tibia; abdomen purple-grey except yellow-white on venter anteriad of epigastric furrow, on booklung covers, and on spinnerets.

Carapace 2.81 long, 2.50 wide, height at

Figures 2–3.—Nests of female *Poecilomigas basilleupi,* Mazumbai, showing camouflaged outer surface of exposed nest wall with attached, open door. Scale = 5.0 mm.
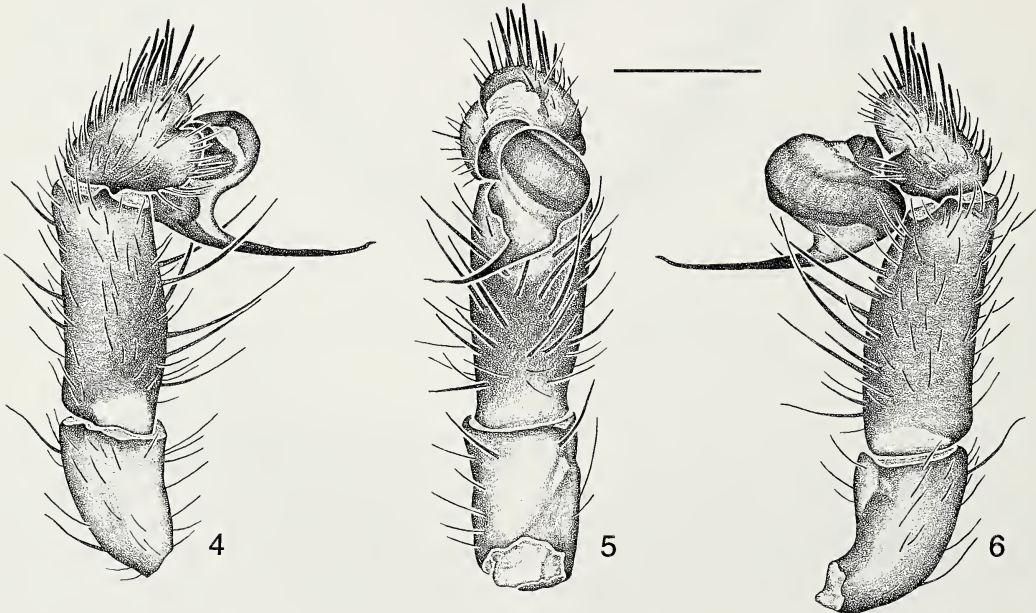
Figures 4–6.—Left male pedipalpus of *Poecilomigas basilleupi,* Mazumbai. 4, Prolateral; 5, Ventral; 6, Retrolateral. Scale = 0.5 mm.
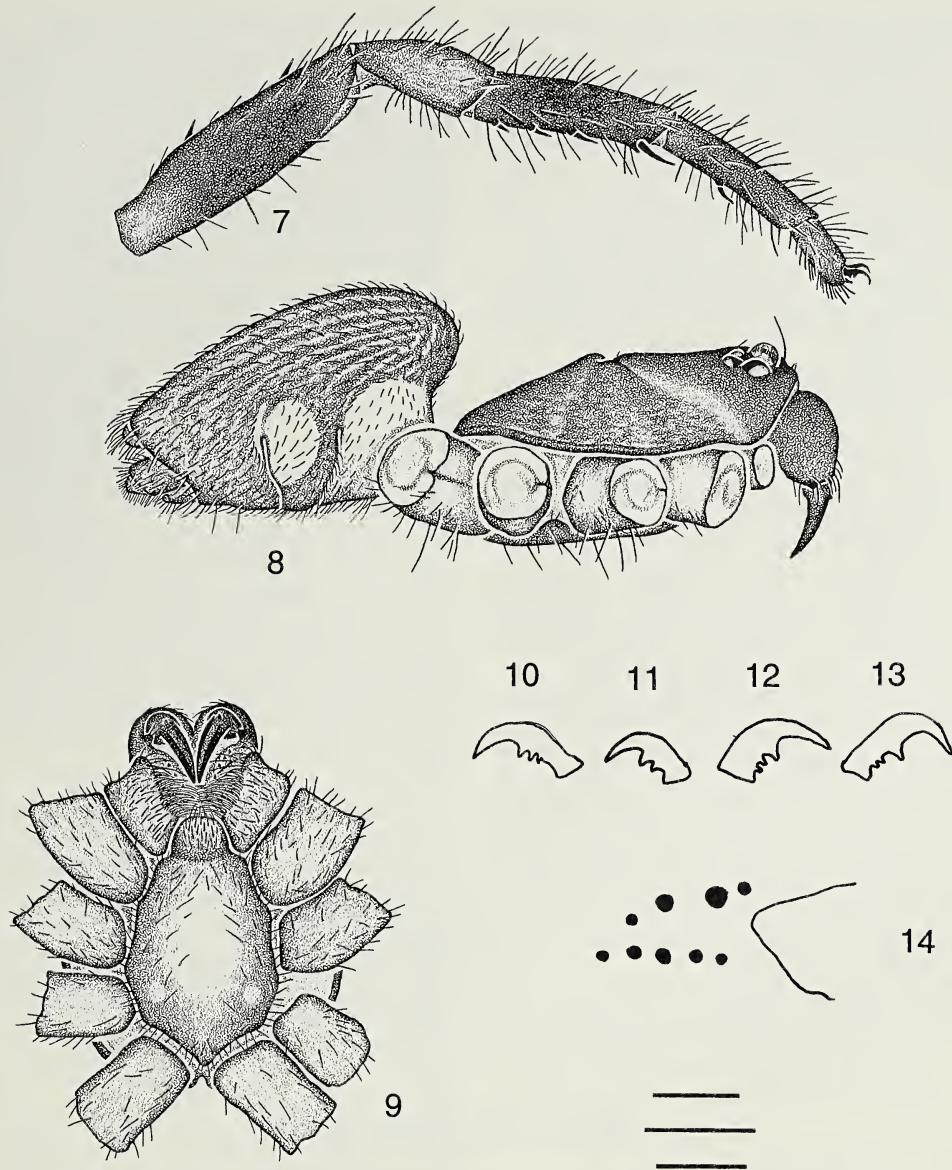
Figures 7–14.—Morphology of male *Poecilomigas basilleupi,* Mazumbai. 7, Leg I, retrolateral; 8, Habitus, lateral; 9, Cephalothorax, ventral; 10, Prolateral STC I; 11, Retrolateral STC I; 12, Prolateral STC IV; 13, Retrolateral STC IV; 14, Cheliceral teeth, schematic, promargin to top. Scale: top bar for 7 = 1.0 mm; middle for 8, 9 = 1.0 mm; bottom for 10–14 = 0.2 mm.

thoracic fovea 0.30× carapace width; weakly rugose. Caput 0.62× carapace width, low (Fig. 8), height at OA equal to that at fovea; with pair of short prefoveal setae but lacking setal rows; one large seta between AME; clypeus 0.45× length OAL, margin weakly curved. Thoracic fovea recurved, width 0.20× that of carapace, 3.20× wider than long.

Ocular area width 0.61× caput, 2.10× wider than long; AER 0.97 wide, 1.07× width PER. Ratio of eyes: AME:ALE:PME:PLE: 2.00:2.14:1.00:1.43, diameter AME 0.22; AME separated by 0.43 of their diameter, PME by 3.43× their diameter. Ocular quadrangle 1.31× wider than long, posterior width 1.22× anterior.

Sternum 1.84 long, 1.42 wide, widest behind coxae II and narrowed anteriorly, sparsely setose laterally; sigilla 0.14× width sternum, round, lateral, distance between 7.00× distance from margin (Fig. 9). Labium and pedipalpal coxae lacking cuspules; labium 0.39 long, 0.52 wide, pedipalpal coxae 0.87 long, 0.58 wide, apex weakly produced. Chelicerae 0.44 long, promargin of fang furrow with small basal, two large median, and one small distal tooth, retromargin with five small teeth (Fig. 14).

Legs sparsely covered with short setae. Femur I 1.02, tibia I 0.70, femur IV 0.90, and tibia IV 0.52× width carapace. Scopulae entire beneath tarsi III and IV and apically on metatarsi III ($\frac{1}{5}$) and IV ($\frac{3}{4}$). Spination: pedipalpus: femur d0–0–1, tarsus 10–12 dorsoapical; leg I (Fig. 7): femur d1–0–1, tibia p0–1–1–0, v1–1–1–1 (all r, apical enlarged); metatarsus v0–1(r)-0; leg II: femur d0–1–1–0, tibia p0–0–1–0, v1- 1–1 (all r); leg III: femur d0–1–0; leg IV: femur d0–1–1–0. Superior tarsal claws with 2–4 basal teeth (Figs. 10–13). Leg measurements (Femur + Patella + Tibia + Metatarsus + Tarsus = [Total]): I: 2.62 + 1.45 + 1.84 + 1.77 + 0.77 = [8.45]; II: 2.29 + 1.29 + 1.64 + 1.58 + 0.71 = [7.51]; III: 1.81 + 1.09 + 1.26 + 1.19 + 0.87 = [6.22]; IV: 2.32 + 1.93 + 1.35 + 1.55 + 1.00 = [8.15]; pedipalpus: 1.45 + 0.74 + 0.93 + (absent) + 0.55 = [3.67].

Pedipalpus (Figs. 4–6) with femur 0.57, tibia 0.36× carapace width; femur 1.55, tibia 1.70× length tarsus; tibia slender, height 0.41× length; bulb width 1.14× tarsus length; embolus length 1.51× bulb width. Abdomen 2.75 long, 2.19 wide, sparsely covered with coarse setae.

Female variation: (encompassing specimens from Mazumbai and Mt. Kilimanjaro; n = 4): Total length 7.60–8.93; height at fovea 0.32–0.36× carapace width. Caput 0.73–0.82× carapace width, flat to inclined, height at AER 0.94–1.12× height at fovea; width ocular area 0.50–0.59× caput width, diameter ALE 1.07–1.50× AME, PLE 1.11–1.28× PME; clypeus length 0.31–0.53× OAL, margin straight to curved, with 4–6 marginal and 5–9 median setae; thoracic fovea width 2.25–3.00× length. Sternal sigilla width 0.13–0.17× sternum width, round to slightly oval; labium with 14–19 cuspules, pedipalpal coxae with 15–23 cuspules; retromargin of fang furrow with 4–6 teeth. Tibia I with 5–7, metatarsus I with 4–5 retroventral spines, tibia II with 2–3 proventral spines. Prolateral STC IV with 1–3 teeth. Spermathecal length 4.00–4.54× diameter, length 0.74–1.47× base width.

Material examined.—TANZANIA: *Tanga Region:* West Usambara Mts., Mazumbai, 4°49'S, 38°30'E, elev. ca. 1400 m, 10–20 November 1995 (C. Griswold, D. Ubick, and N. Scharff) 1♂1♀ (CAS), 2♀ (ZMUC). *Kilimanjaro Region:* Mt. Kilimanjaro, Marungu, SE slopes, elev. 1800–2200 m, 20–27 July 1957 (P. Basilewsky & N. Leleup) 1♀ (MRAC #112228) (holotype of *Poecilomigas basilleupi*).

KEY TO SPECIES OF *POECILOMIGAS*

1. Males 2
   Females 4
2(1). Dorsum of abdomen pale, with anteromedian dark diamonds and posterior chevrons (Griswold 1987b: fig. 62); pedipalpal tibia relatively stout, height greater than 0.50× length; embolus elongate, length greater than 1.80× bulb width (Griswold 1987b: fig. 61) . .*elegans* Griswold 1987
   Dorsum of abdomen dark (Figs. 1, 8; Griswold 1987b: figs. 2, 33); pedipalpal tibia relatively slender, height less than 0.45× length (Fig. 6); embolus length less than 1.60× bulb width. . . . 3
3(2). Dorsum of abdomen with broad, dark median band, middle of sides pale (Griswold 1987b: figs. 2, 33); with at least weak scopulae beneath tarsi I (Griswold 1987b: fig. 35) and II . . . .
   . . . . *abrahami* (O.P. Cambridge 1889)
   Dorsum and sides of abdomen entirely dark (Figs. 1, 8); scopulae absent from tarsi I (Fig. 7) and II. . . . . *basilleupi* Benoit 1962
4(1). Dorsum and sides of abdomen entirely dark (Griswold 1987b: fig. 47); spermathecae straight, length less than 4.80× diameter (Griswold 1987b: fig. 46) . . . . *basilleupi* Benoit 1962
   Dorsum of abdomen with broad, dark median band, middle of sides pale (Griswold 1987b: figs. 1, 22); spermathecae of most specimens sinuate, length greater than 5.00× diameter (Griswold 1987b: figs. 41–45) . . . . *abrahami* (O.P. Cambridge 1889)

NATURAL HISTORY

Six nests of *Poecilomigas basilleupi* were observed at Mazumbai, and three collected and measured. All were vertically oriented on tree trunks or stumps (Figs. 2–3) and located in a crack or depression so that the exposed nest wall protruded out slightly or not at all from the surrounding bark. Each had a single thin, flexible, wafer door at the upper end attached by a horizontal hinge that was located on the exposed wall of the nest. The outer surface of the exposed wall incorporated bits of the surrounding substrate (e.g., lichen, bark and moss) such that the silken weave was not visible, effecting excellent camouflage (at least to human eyes). The outer surface was rough like bark but flexible, and felt like a soft spot on the bark. The inner surfaces of the nest and door were lined with a densely woven layer of off-white silk. The hidden wall of the nest that attaches to the bark was thinner than the exposed wall and had gaps exposing parts of the inner chamber directly to the bark. The dimensions (in mm) of these nests ($n = 3$), each of which contained a mature female, were ($\bar{x}$: min–max) length (21.67: 18.0–24.0), width (11.67: 10.0–14.0), depth (7.33: 6.0–8.0), door length (7.17: 6.5–8.0), and door width (9.00: 7.0–10.0). Doors were broadly oval, ratio of width/length = 1.07–1.43; the length of the nest was 2.37–2.67× the length of the occupant. A single male was found wandering at midnight on the trunk of a *Ficus* tree where occupied nests had been observed. The nests observed occurred on trees and stumps forming hedgerows along the edges of fields and small roads. No concerted effort was made to locate nests in undisturbed forest, and the occurrence of *P. basilleupi* in such forest is possible.

DISCUSSION

In addition to having the diagnostic strikingly banded tibiae and metatarsi typical of both sexes, males of *Poecilomigas abrahami* and *P. elegans* were diagnosed from males of *Migas* by having scopulae beneath at least some tarsi and dorsal femoral spines short to absent (Griswold 1987b). This diagnosis works for males of *P. basilleupi* as well.

The single door nests of *Poecilomigas basilleupi* resemble those recorded for *Calathotarsus* Simon 1903 (Schiapelli & Gerschman de Pikelin 1973), *Migas* L. Koch 1873 (Wil-

ton 1968) and *Moggridgea* O.P. Cambridge 1875 (O.P. Cambridge 1875; Griswold 1987a). They differ from the nests typical of *P. abrahami,* which have a door at each end, suggesting that the latter behavior may be derived.

LITERATURE CITED

Benoit, P.L.G. 1962. Migidae nouveaux du Musée Royal de l'Afrique Central. Rev. Zool. Bot. Africaines, 66:276–282.

Bonnet, P. 1958. Bibliographia Araneorum. Toulouse, 2(4):3027–4230.

Brignoli, P.M. 1983. A catalogue of the Araneae described between 1940–1981. Manchester, 755 pp.

Cambridge, O.P. 1875. On a new genus and species of trapdoor spider from South Africa. Ann. Mag. Nat. Hist., 4(16):317–322.

Cambridge, O.P. 1889. On some new species and a new genus of Arachnida. Proc. Zool. Soc. London, 1889:34–46.

Griswold, C.E. 1987a. The African members of the trap-door spider family Migidae (Araneae: My-

galomorphae), 1: The genus *Moggridgea* O.P. Cambridge, 1875. Ann. Natal Mus., 28:1–118.

Griswold, C.E. 1987b. The African members of the trap-door spider family Migidae (Araneae: Mygalomorphae), 2: The genus *Poecilomigas* Simon. Ann. Natal Mus., 28:475–497.

Koch, L. 1873. Die Arachniden Australiens, nach der Natur beschrieben und abgebildet. Nürnburg, 1873:369–472.

Platnick, N.I. 1989. Advances in spider taxonomy: a supplement to Brignoli's A Catalogue of the Araneae described between 1940 and 1981. Manchester, 673 pp.

Redhead, J.F. 1981. The Mazumbai Forest: an island of lower montane rainforest in the West Usambaras. African J. Ecol., 19:195–199.

Roewer, C.F. 1942. Katalog der Araneae von 1758 bis 1940. Bremen: Natura, 1:1–1040.

Scharff, N., C. Griswold, & D. Ubick. 1996. Biodiversity and biogeography of the spider fauna of the Eastern Arc Mountains, Tanzania: preliminary report. Tanzania Commission Sci. & Tech., Dar es Salaam, 10 pp.

Schiapelli, R.D. & B.S. Gerschman de Pikelin. 1973. La Familia Migidae Simon 1892 in la Argentina (Araneae, Theraphosomorphae). Physis, Buenos Aires, 32:289–294.

Simon, E. 1889. Voyage de M.E. Simon au Venezuela (décembre 1887–avril 1888). 4 mémoire. Arachnides. Ann. Soc. Entomol. France, 6(9): 169–220.

Simon, E. 1903. Description d'Arachnides nouveaux. Ann. Soc. Entomol. Belgique, 47:21–39.

Wilton, C.L. 1968. Migidae. Pp. 74–126, *In* The spiders of New Zealand, Part II. (R.R. Forster & C.L. Wilton, eds.). Otago Museum Bulletin.

SALTICIDAE OF THE PACIFIC ISLANDS. III. DISTRIBUTION OF SEVEN GENERA WITH DESCRIPTIONS OF NINETEEN NEW SPECIES AND TWO NEW GENERA

James W. Berry: Department of Biological Sciences, Butler University, Indianapolis, Indiana 46208 USA

Joseph A. Beatty: Department of Zoology, Southern Illinois University, Carbondale, Illinois 62901-6501 USA

Jerzy Prószyński: Muzeum i Instytut Zoologii PAN, ul. Wilcza 64 00–679 Warszawa, Poland

ABSTRACT. This is the third paper in a series on the jumping spiders (Araneae, Salticidae) of the Pacific Islands. It includes the genera *Cytaea, Hasarius, Menemerus, Pseudicius, Sobasina,* and the new genera *Lakarobius* and *Xenocytaea.* It describes 19 new species: *Cytaea carolinensis, C. koronivia, C. nausori, C. ponapensis, C. rai* and *C. vitiensis; Lakarobius alboniger; Sobasina aspinosa, S. coriacea, S. cutleri, S. magna, S. platypoda, S. yapensis* and *S. paradoxa; Xenocytaea daviesae, X. triramosa, X. anomala, X. maddisoni* and *X. zabkai. Pseudicius samoaensis* is synonymized with *P. kraussi.* A key to the species of *Sobasina* is provided. Types of all new species are deposited in the Bishop Museum (BPBM) in Honolulu, Hawaii, except for *S. cutleri* which is in the American Museum of Natural History in New York.

This is the third paper in a series on the jumping spiders (Araneae, Salticidae) of the Pacific Islands (see Berry, Beatty & Prószyński 1996, 1997) and the last to describe new taxa. The genera included here are *Cytaea* Keyserling 1882, *Hasarius* Simon 1871, *Menemerus* Simon 1868, *Pseudicius* Simon 1885, *Sobasina* Simon 1898 and the new genera *Lakarobius* and *Xenocytaea.* Nineteen new species are described: *Cytaea carolinensis, C. koronivia, C. nausori, C. ponapensis, C. rai, C. vitiensis, Lakarobius alboniger, Sobasina aspinosa, S. coriacea, S. cutleri, S. magna, S. platypoda, S. yapensis* and *S. paradoxa;* and *Xenocytaea anomala, X. daviesae, X. maddisoni, X. triramosa* and *X. zabkai.*

The newly described species are from the Caroline Islands (Palau, Ponape, Truk and Yap), Fiji and Tonga. Almost all of them are known at present from single islands or compact groups of islands. The genus *Cytaea* is found from Burma and the Philippines through Indonesia and Melanesia to Australia, Fiji and Samoa. It has not previously been recorded from Micronesia. *Sobasina,* previously known only from central Melanesia (Wanless

1978), is newly recorded from the Caroline Islands, Fiji and Tonga. The genus *Pseudicius* is widespread and known from all zoogeographic regions of the Old World. Two genera, *Hasarius* and *Menemerus,* are each represented by a single well-known pantropical to nearly cosmopolitan species. Both have been described and illustrated repeatedly (e.g., Davis & Żabka 1989), and we give only new distribution records.

Some justification is needed for the description of the new genera *Lakarobius* and *Xenocytaea* "in a family which is almost certainly overloaded with generic synonyms" (Wanless 1984) and "given the overabundance of obscure genera in salticids" (Maddison 1996). An exhaustive literature search through about 150 described genera of salticids, including all those from Australia and the whole tropical Pacific, has not turned up any genus into which these species would fit. There seems to be no alternative to describing new genera under this circumstance. We have been unable, however, to examine specimens of all of the described genera. It is possible that some lesser known genus might turn out to be synonymous with either *Xenocytaea* or *Lakarobius.*

At first we intended to place these species in *Cytaea* because of their similarity in palpal structure. However, the palps of *Cytaea,* as is often the case with the relatively simple palps of many salticids, are not really distinctive. They are rather closely matched in other genera such as *Ascyltus* Karsch 1878, *Canama* Simon 1903, *Euryattus* Thorell 1881 and *Servaea* Simon 1887. The epigyna of most of the species of *Xenocytaea* (except *anomala*) are of an entirely different form from those in *Cytaea*. In *Cytaea* the retromarginal cheliceral tooth is broad, with a crescentic distal margin; in *Xenocytaea* (except *anomala*) it is narrow and bifurcate distally. The cheliceral promargin in *Cytaea* has four to five teeth, in *Xenocytaea* only two. There are differences in the leg spination between the two genera. For example, *Cytaea* has 3–3 ventral spines on tibia I, *Xenocytaea* has 2–2 (except, again for *anomala*). The color pattern characteristic of most *Cytaea,* especially that of the male, does not occur in *Xenocytaea*. The four-cusped retromarginal cheliceral tooth, absence of lateral spines from metatarsus I and non ant-like form distinguish *Lakarobius* from all other salticid genera in the entire tropical Pacific and Australia.

The collections on which this paper is based were mostly made by J.W. Berry, E.R. Berry, and J.A. Beatty (indicated as JWB, ERB, and JAB in the text) in a series of collecting trips: Marshall Islands (1968, three months; 1969, three months); Palau (1973, six months); Guam, Yap, Truk, Ponape, Taiwan (1973, 1–2 weeks each); Yap (1980, six months); Marquesas, Tuamotu, Society, Cook and Fiji Islands (1987, six months total); and Hawaii (1995, 1997, 1998, three months). Specimens were borrowed from the Bishop Museum (BPBM) and the American Museum of Natural History (AMNH) and are occasionally referred to. The generic diagnoses are intended to distinguish only among salticid genera reported from the Pacific Islands (Micronesia and Polynesia), excluding the large islands near Asia and Australia, the sub-Antarctic and the eastern Pacific Islands. In the descriptions, genera are categorized by size as follows: small, 2–4 mm total length; medium, >4–8 mm; large, >8–16 mm; and very large, over 16 mm. All measurements are in millimeters. Illustrations of male palpi are of the left palp unless otherwise stated. Ventral leg spination

is described as two longitudinal spine rows, the outer row given first, e.g., 5–4 indicates 5 spines in the outer row and 4 spines in the inner row, 3 to 5–4 to 6 gives the range of variation in each row, outer row first.

The holotypes of all new species are deposited in the Bishop Museum (BPBM) (State Museum of Hawaii) in Honolulu, except that of *Sobasina cutleri,* which is in the AMNH. Representatives of some of the species will be deposited in the U.S. National Museum (Washington) and the Florida State Collection of Arthropods (Gainesville). All adult specimens are paratypes unless specifically excluded in the text; juveniles are not paratypes.

Genus *Cytaea* Keyserling 1882

Type species *Cytaea alburna* Keyserling 1882. Syntypes from Australia in Zool. Staatsinst. und Zool. Mus. Hamburg.

Discussion—. This genus contains 30 described species known from the Philippines and southeast Asia to Australia and Samoa. It has not been reported previously from Micronesia. It resembles the other genera in Simon's (1903) Cytaeae and Servaeae in a number of respects, but is clearly distinguished from them by the characters given in the diagnosis. Simon described the Cytaeae as scarcely differing from the Hasarieae except by having more than two promarginal cheliceral teeth, but some features of the cytaeine leg spination differ from the spination in *Hasarius*.

Diagnosis.—Retromargin of chelicera with a two-cusp tooth, the cusps of equal size, promargin with 3 to 6 (usually 4 to 5) teeth. All tibiae, patellae and metatarsi normally with lateral spines; rarely metatarsus I lacks them. Tibiae each with a dorsal spine near base, sometimes lacking on tibiae I and II.

The only similar genera in the entire Pacific are *Ascyltus, Euryattus* and *Servaea,* only the first of which occurs in the area considered here. Males of all three of these have the tibia of the palp 1.25–4× as long as wide. In *Cytaea* both tibia and patella are very short, as wide as long or wider. *Ascyltus* has anterolateral patches of iridescent scales on the carapace, lacking in *Cytaea.* The epigynal septum of *Servaea* is much wider than that of *Cytaea.* The epigynal fossa of *Euryattus* has an internal sclerotized pouch, extending forward from its anterior margin, that of *Cytaea* does not.

Descriptive notes.—Fissident salticids
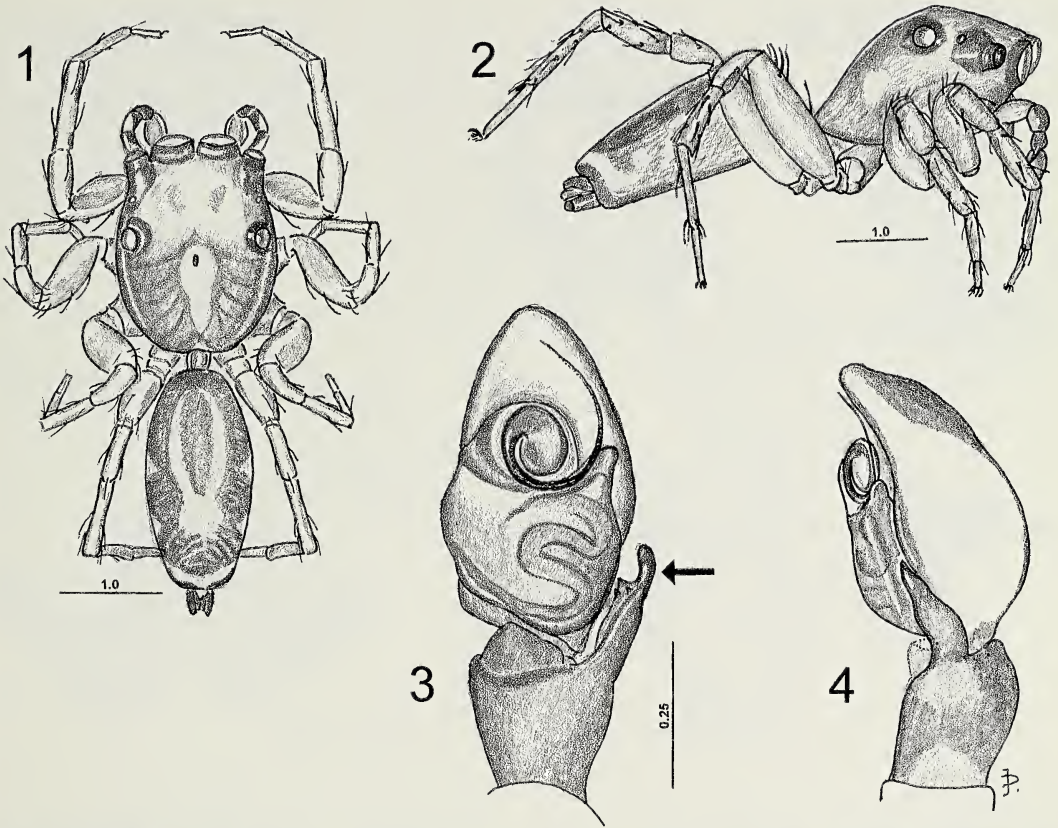
Figures 1–4.—*Cytaea piscula* from American Samoa. 1, General appearance of male; 2, Lateral view of male; 3, Palp ventrally, with arrow indicating distal notch; 4, Palp laterally.

with cephalothorax high, not widened anteriorly, cephalic region nearly flat; thoracic groove present; ocular region equal in length to thoracic region or somewhat shorter. Ocular quadrangle parallel-sided, wider than long. Anterior eye row straight or slightly recurved, eyes equidistant; ALE diameter half that of AME. Second eye row halfway between first and third rows. PLE large, located about their diameter from the PME. Posterior slope of thoracic region gradual. Clypeus and base of chelicerae densely hairy. Chelicerae small in both sexes, with 3 to 6 (usually 4 or 5) promarginal teeth and one retromarginal tooth with two cusps. Sternum ovate, broadly truncate anteriorly. First coxae separated by the width of the labium or more. Labium longer than wide. Leg formula III=IV-I-II. Tibia I with 3–3 ventral spines, lateral spines present on both sides. Metatarsus I with 2–2 ventral spines, lateral spines usually present on both sides.

Epigynum often with two large oval membranous "windows"; ducts forming loops which usually lie almost entirely posterior to the windows. In some species the windows are smaller and round, the external appearance of the epigynum then resembling that of *Ascyltus* species. A median septum between the windows varies from very narrow to about ⅔ of the diameter of one of the windows. Palp with sinuous reservoir, embolus coiled flat on the anterior part of the bulb ventrally or three-dimensionally at the anterior end of the bulb (Figs. 3, 8). A characteristic color pattern is common to several species (Figs. 5, 18): *C. alburna* Keyserling 1882, *C. frontaligera* (Thorell 1881), *C. mitellata* (Thorell 1881), *C. nimbata* (Thorell 1881) and the six new species described below. A somewhat different pattern is present in *C. flavolineata* (Berland 1938) and *C. piscula* (L. Koch 1867) (Figs. 1, 2). Ventral coloration whitish to whitish-yellow.

Map 1.—Major island groups in the Pacific Ocean.

Cytaea piscula (L. Koch 1867)
Figs. 1–4, Map 2

Attus pisculus L. Koch 1867, p. 224.
Cytaea piscula (L. Koch): Berland 1929, p. 73.

Map 2.—Distribution of seven species of *Cytaea* in the Pacific. *Cytaea piscula* (★), *Cytaea carolinensis* new species (●), *Cytaea koronivia* new species (♦), *Cytaea nausori* new species (▲), *Cytaea ponapensis* new species (□), *Cytaea rai* new species (○), and *Cytaea vitiensis* new species (■).

Discussion.—The palps of our specimens agree with that of the type specimen, whose unpublished drawing was made available by Dr. M. Żabka. Embolus coiled flat on ventral surface of bulb, its basal width less than half width of bulb (Fig. 3). In this it resembles *C. rai* new species and *C. vitiensis* new species. It is distinguished from these by the retrolateral tibial apophysis of the palp which extends forward to near middle of bulb and in ventral view shows a distal notch (Fig. 3).

Description.—*Male:* (*n* = 2). Total length 4.5, 4.7; length of carapace 1.9, 2.2; maximum carapace width 1.5, 1.7; eye field length 1.2, 1.3; eye row I width 1.5, 1.5. *Legs:* Leg formula 4–3–1–2, patella-tibia III=IV. Patella-tibia I length 1.6 (*n* = 1).

Material examined.—AMERICAN SAMOA: *Tutuila,* Fagatogo, 2♂ 1imm, 14 July 1973 (JAB).

Distribution.—Samoa.

Cytaea carolinensis new species
Figs. 5–12, Map 2

Holotype.—Male holotype from Caroline Islands, Palau, Malakal Island, dry tropical forest, tree shaking, 14 March 1973, (J.W. Berry & J.A. Beatty) (BPBM).
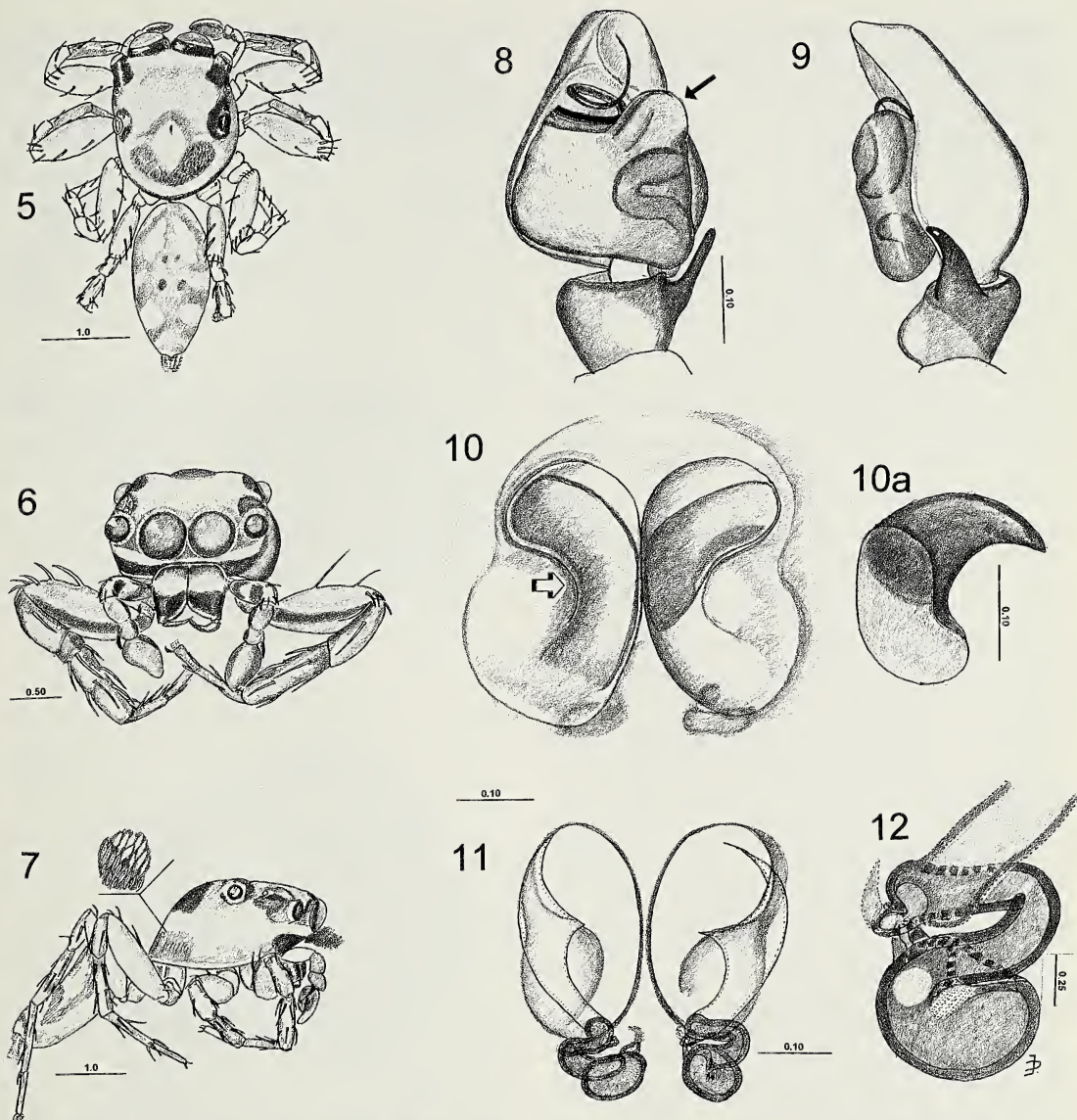
Figures 5–12.—*Cytaea carolinensis* new species from Palau, Caroline Islands. 5, Holotype male, dorsal appearance; 6, Holotype male, frontal appearance; 7, Holotype male, lateral appearance; 8, Palp ventrally of holotype, with arrow showing projection of bulb lateral to embolus; 9, Palp laterally; 10, Epigynum with entrances and grooves blocked by waxy material, with arrow indicating heavily sclerotized insemination duct; 10a, Waxy plug removed from epigynum; 11, Internal structure of epigynum after removal of material from the copulatory opening; 12, Left single spermatheca and duct (note junction of unsclerotized and sclerotized parts of the duct).

Etymology.—The species is named for the Caroline Islands, where it was collected.

Diagnosis.—Differs from most other *Cytaea* in palpal structure (Figs. 8, 9), but corresponds with male of *C. ponapensis* new species (Fig. 21) by having the embolus forming a three-dimensional spiral at the anterior end of the bulb, rather than a flat coil on the ven-

tral surface. The smaller loop of the embolus and anterior projection of the bulb lateral to embolus distinguish it from *ponapensis* (Fig. 8). The female is similar to *C. ponapensis* new species and *C. rai* new species in having the epigynal fossae longer than wide and the insemination ducts posterior to the fossae. It is distinguished by having the fossa margin in-

distinct and the external part of the insemination duct heavily sclerotized, giving an appearance of two C's facing in opposite directions (Fig. 10).

Description.—*Male:* (*n* = 5). Total length 4.1–5.1 ($\bar{x}$ = 4.67), length of carapace 2.1–2.5 ($\bar{x}$ = 2.24), maximum carapace width 1.5–1.7 ($\bar{x}$ = 1.58), eye field length 1.1–1.3 ($\bar{x}$ = 1.23), eye row I width 1.5–1.8 ($\bar{x}$ = 1.63). Cephalothorax light yellow, with black around lateral eyes; a brown semicircular spot on thoracic region, bordered anteriorly by a light transverse band and posteriorly by a distinct white band on the posterior slope; a dark band on posterior margin (Fig. 5). Sides of cephalothorax whitish-yellow, with marginal band of light-brown scales (Fig. 7) and thin, whitish line along the ventral edge. Abdomen light brown, with indistinct pattern of white and dark spots. Clypeus with an anterior line of small white scales and darker edge; three darker yellow triangles between anterior eyes and the band of white scales. Basal and apical surfaces of chelicerae dark brown (Fig. 7), separated by transverse band of white setae. A dark spot apically on prolateral surface of pedipalpal femur. *Legs:* Whitish; a dark band along anterior surface of femur I and dark ventral surface of tibia I and patella I in some specimens. Leg formula 3–4–1–2; patella-tibia III = IV. Patella-tibia I length 1.55–1.8 ($\bar{x}$ = 1.69). *Palp:* Short and broad, triangular, embolus located anteriorly and twisted into a coil, seminal reservoir ducts sinuous, but limited to retrolateral half of the bulb; apophysis of medium length, ventrally appears as a narrow plate, rounded apically, laterally hook-like; tibia short (Figs. 8, 9).

Female: (*n* = 5). Total length 5.5–6.5 ($\bar{x}$ = 5.93), length of carapace 2.5–2.7 ($\bar{x}$ = 2.59), maximum carapace width 1.9–2.1 ($\bar{x}$ = 1.91), eye field length 1.3–1.5 ($\bar{x}$ = 1.43), eye row I width 1.7–1.9 ($\bar{x}$ = 1.82). Body shape and proportions resembling male, pale without distinct contrasts. Cephalothorax yellowish with slightly darker yellow eye field, lateral eyes black-rimmed, with a few colorless scales on eye field. Abdomen covered with minute brownish scales and small spots of whitish scales that also make an oval anterior spot; abdomen ventrally white, covered by colorless scales. Frontal aspect light fawn, with eyes rimmed dorsally with white scales, more conspicuous than in male; a transverse

belt of dense white setae and scales along clypeus, chelicerae yellowish-fawn, with a spot of whitish setae medially. Ventral aspect light. Pedipalpal femur and patella white. *Legs:* Yellow, tibia and tarsus light fawn with sparse long colorless setae. Femur I without dark band. Leg formula 3–1=4–2; patella-tibia III=IV. Patella-tibia I length 2.0–2.3 ($\bar{x}$ = 2.10). *Epigynum:* Elongate oval with two oval depressions separated by a thin, sclerotized ridge, a circular area anteriorly in each depression, delimited posteriorly by a broad ridge of funnel-shaped copulatory opening (Figs. 10–12). Copulatory duct not sclerotized distally, and leading to a sclerotized transverse loop which merges with an oval spermathecal chamber (Fig. 12).

Material examined.—CAROLINE ISLANDS: *Palau,* Malakal, dry tropical forest, tree shaking, 6♂ (including holotype) 1♀, 14 March 1973 (JWB & JAB). Rock Island east of Malakal, dry tropical forest, elev. 100 ft., curled up leaf, 1♀, 8 March 1973 (JWB). Rock Island east of Malakal, tree shaking, 1♀ 4imm, 9 February 1973 (JWB). Koror, Japanese temple ruins, tree shaking, 1♂, 14 March 1973 (JAB & JWB). Koror, scrub forest in vacant lot, tree shaking, 1♂, 13 March 1973 (JAB & JWB). Koror, in cave entrance, 1♂, 13 March 1973 (JAB & JWB). Arakabesan Island, mixed tropical forest, elev. 50–70 ft., tree shaking, 2♂ 3imm, 16 February 1973 (JWB). Arakabesan Island, dry tropical forest, elev. 374 ft., tree shaking, 1♂1♀, 1 March 1973 (JWB). Arakabesan Island, mixed tropical forest, 2♀, 1 March 1973 (JWB). Angaur, roadside bushes, 1♂1♀, 28 April 1973 (JWB & JAB). Babelthuap, Airai, lowland tropical forest, north of airstrip, 1♂ 1imm, 27 March 1973 (JAB & JWB). Babelthuap, below forestry headquarters at Nekkin, mixed tropical forest in open, shaking trees, 4♂1♀ 2imm, 3 February 1973 (JWB). Babelthuap, Ngaremlengui, in woods, 1♂2♀ 3imm, 21 April 1973 (JWB & JAB). Babelthuap, Ngaremlengui, grass field, sweeping, 1♀ 1imm, 21 April 1973 (JAB & JWB). Babelthuap, Airai, tree in field, 1♂1♀ 1imm, 7 May 1973 (JAB & JWB). Babelthuap, Airai, below SDA school, dry tropical forest, 1♂1♀ 1imm, 10 March 1973 (JAB & JWB). Peleliu, mixed tropical forest, 4♂, 22 March 1973 (JWB). *Truk,* Moen, tree shaking, quarry hill, 1♂ 1imm, 12 June 1973 (JAB & JWB).

Distribution.—Known from Truk and the Palau group in the Caroline Islands.

Cytaea koronivia new species
Figs. 13–15, Map 2

Holotype.—Holotype female from Fiji, Viti Levu, 22.4 km W of Suva, 5 May 1980 (J.W. Berry & E.R. Berry) (BPBM).
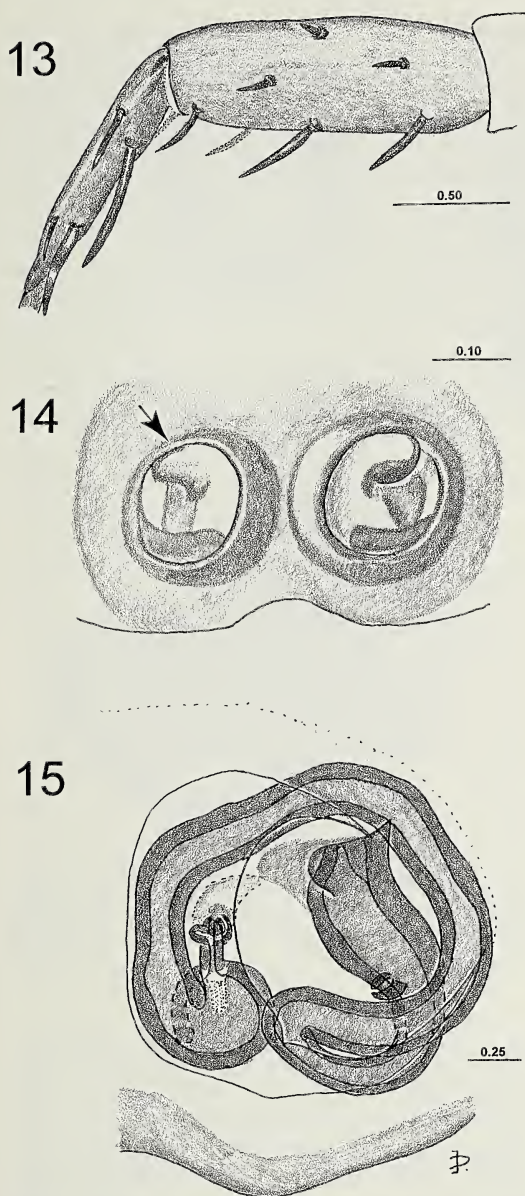
Figures 13–15.—Holotype female of *Cytaea koronivia* new species from Viti Levu, Fiji. 13, Tibia I retrolaterally (note reduction in size of lateral spines); 14, Epigynum, with arrow indicating copulatory opening near anterior margin; 15, Internal structure of epigynum with left spermatheca and ducts.

Etymology.—The name *koronivia* is a noun in apposition after the locality where the first specimen was collected.

Diagnosis.—Epigynal fossae round or slightly longer than wide, septum wide. Resembles *C. subsiliens* Kulczynski 1910 (Prós-

zyński 1984) but has the copulatory openings nearer the anterior margin of the epigynum (Fig. 14). The duct of the epigynum differs from that of other species by almost completely encircling one of the round windows before entering the globular spermatheca (Fig. 15).

Description.—*Female: (n = 2)*. Total length 7.3, 7.6; length of carapace 2.9, 3.1; maximum carapace width 2.2, 2.5; eye field length 1.7, 1.7; eye row I width 2.1, 2.2. Cephalothorax dorsally light brown, with arrowhead-shaped whitish spot just behind fovea; eye field fawn, covered with minute colorless scales, limited posteriorly by a row of brown scales, thoracic region medially with dark brown and whitish scales, sides and posterior slope yellow with sparse whitish scales. Black areas around lateral and anterior eyes, covered with whitish and a few reddish scales. Abdomen light greyish-yellow with indistinct pattern of lighter pairs of diagonal spots covered with colorless scales, and separated by lines of slightly darker, brownish scales. Frontal aspect without any contrasting spots, pale fawn, with area around AME brown, eyes surrounded with whitish setae, clypeus very low with whitish setae above chelicerae. Chelicerae brownish-yellow; pedipalps with femora whitish, patella and tibia yellow, tarsus light brown, all covered with whitish setae. *Legs:* Prolateral surfaces of femora I whitish, remaining segments yellow to light brown, yellow on legs II-IV. Tibia I-II with three lateral spines on each side, retrolateral spines much shorter than the others; metatarsi I-II with 2–2 ventral spines and two lateral spines on each side; legs III-IV spines long or only slightly shortened on tibiae. Leg formula 4–1=3–2; patella-tibia III = IV. Patella-tibia I length 2.2, 2.4. *Epigynum:* With two circular "windows", the ducts forming a circle dorsal to the windows, spermatheca globular (Figs. 14, 15).

Male: The male is unknown.
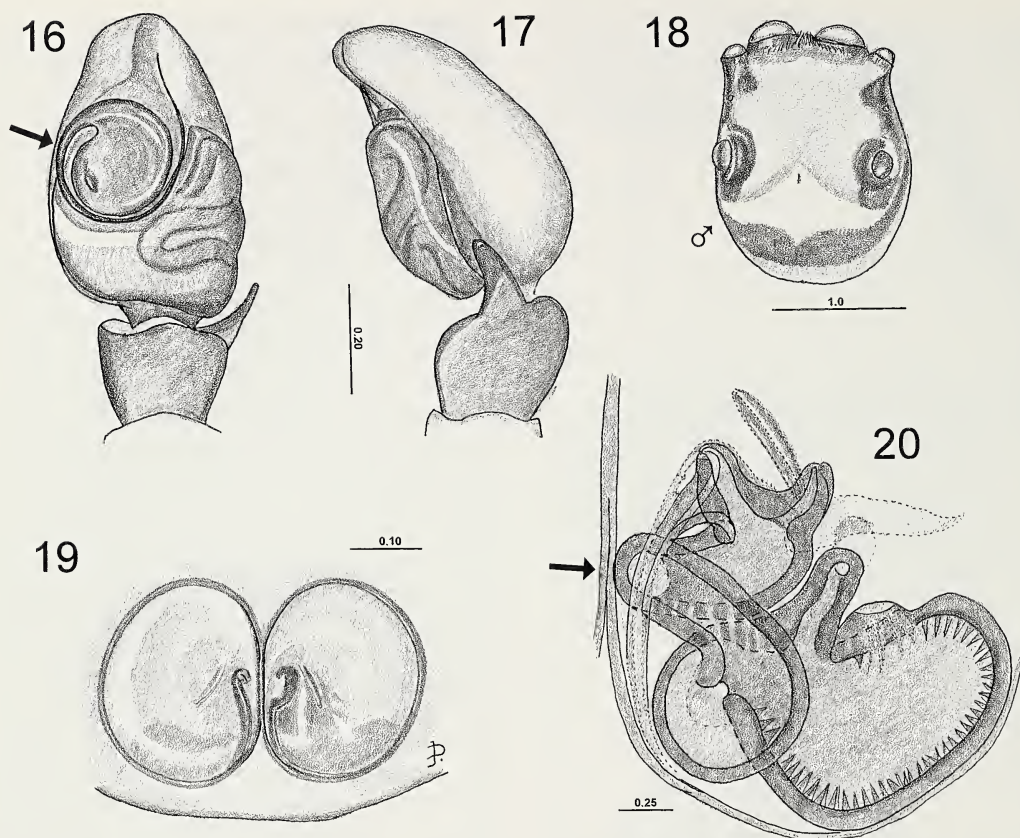
Material examined.—FIJI: *Viti Levu,* 22.4 km W of Suva City, forest, sweeping and shaking, 1♀ (holotype), 5 May 1987 (JWB, ERB). Nausori, Koronivia Research Station, on tree trunk, 1♀, 19 May 1980 (JAB).

Distribution.—Known only from Viti Levu, Fiji.

Cytaea nausori new species
Figs. 16–20, Map 2

Holotype.—Holotype male from Fiji, Viti Levu, Nausori Highlands Forest Preserve,

Figures 16–20.—*Cytaea nausori* new species from Viti Levu, Fiji. 16, Palp of holotype ventrally, with arrow indicating wide coiled base of embolus; 17, Palp of holotype laterally; 18, Dorsal pattern of holotype male cephalothorax; 19, Epigynum; 20, Internal structure of left side of epigynum, with arrow indicating duct forming two loops.

Leuve-i-toko Block, elev. 1500 ft., shaking and hand collecting, 27 May 1987 (J.W. & E.R. Berry) (BPBM).

Etymology.—The name is a noun in apposition after the area where the type specimen was collected.

Diagnosis.—The embolus of the palp is coiled flat on the bulb, its circular base almost ½ of the bulb width (Figs. 16, 17). The epigynum has two circular windows separated by a linear septum (Fig. 19), resembling that of *C. vitiensis* new species from which it differs by having the duct forming two loops (Fig. 20) rather than one.

Description.—*Male: (n = 1).* Total length 4.3, length of carapace 2.0, maximum carapace width 1.5, eye field length 1.1, eye row I width 1.5. Cephalothorax covered with semi-transparent brownish and colorless scales. There are two transverse marginal spots of

whitish scales anterior to PLE. Eye field light fawn, PLE encircled with whitish scales ventrally and anteriorly, with reddish scales posteriorly and dorsally, PME surrounded with reddish scales covering black pigmented area. There is a spot of white scales between PME and PLE with three transverse bands across the thoracic region behind the eyes: a flattened diamond-shaped upper white band; a median broad band of dense, blackish-brown scales; and a lower, marginal row of whitish scales, extending along sides beneath lateral eyes (Fig. 18). Ventral edge of carapace brown. A row of long flattened whitish scales behind anterior eyes, and behind junction of AME a few orange ones. Abdomen whitish, covered sparsely with small, orangish scales, replaced by whitish ones along median line. A few sparse dark setae scattered over the abdomen. Frontal aspect differs from *Cytaea carolinen-*

sis new species (Fig. 6) by absence of transverse white and dark belts. Face light brown, clypeus very low, light brown without contrasting scales; chelicerae slender, short, light brown, apically yellow; pedipalps greyish-yellow, with tibia and cymbium light brown. Prolateral surface of femur I whitish, with a faint darker ring near apical end, with no other dark marks. *Legs:* Femora whitish, with transverse darkening apically on femur I, remaining segments yellow, with two indistinct darker brown annuli on tibia I. Leg formula 4–3=1–2, patella-tibia III=IV. Patella-tibia I length 1.5. *Palp:* Embolus coiled flat on bulb with a large circular base, retrolateral apophysis a long slightly curved bluntly rounded triangle (Figs. 16, 17).

Female: (n = 1). Total length 5.9, length of carapace 2.1, maximum carapace width 1.8, eye field length 1.3, eye row I width 1.6. Whitish, with cephalothorax and abdomen covered with minute orange scales, with no contrasting pattern; lack of scales on lower sides of cephalothorax and abdomen leaves these areas whitish. Lateral eyes, on black pigmented spots, are surrounded with whitish scales; a row of elongate colorless or orange scales above eyes. Frontal aspect pale yellowish without contrasting marks. *Legs:* Patella-tibia I length 1.7; uniformly whitish, with tibiae-tarsi yellow. Leg formula 4–3–1–2, with patella-tibia III=IV. *Epigynum:* As described in diagnosis *(Figs. 19, 20).*

Material examined.—**FIJI:** *Viti Levu,* Nausori Highlands Forest Preserve, Leuve-i-toko Block, elev. 1500 ft., shaking, picking, 1♂ (holotype) 1♀, 27 May 1987 (JWB & ERB).

Distribution.—Known only from Viti Levu in Fiji.

Cytaea ponapensis new species
Figs. 21–25, Map 2

Holotype.—Male holotype from the Caroline Islands, Ponape, E. of Kolonia, breadfruit/ivory nut forest. 8 June 1973 (J.W. Berry & J.A. Beatty) (BPBM).

Etymology.—Named after the island of Ponape (Pohnpei) in the Caroline Islands where the specimens were collected.

Diagnosis.—Resembles *C. carolinensis* new species in genitalia and *C. rai* new species in color pattern. The male differs from *C. carolinensis* by the wider coil of the embolus

and absence of a projection of the bulb lateral to the embolus (Fig. 21). The three-dimensional apical coil of the embolus (Fig. 21) separates it from *C. rai.* The female has the margins of the epigynal fossae distinct and the anterior portions of the fossae obliquely divergent (Fig. 23). The epigynum of *C. rai* is larger, has parallel fossae and a widening of the septum near its middle (Fig. 28), while that of *C. carolinensis* has indistinct fossal margins and "c" shaped fossae (Fig. 10).

Description.—*Male: (n = 4).* Total length 4.3–4.8 (x̄ = 4.54), length of carapace 2.1–2.2 (x̄ = 2.15), maximum carapace width 1.4–1.5 (x̄ = 1.46), eye field length 1.1–1.3 (x̄ = 1.21), eye row I width 1.4–1.5 (x̄ = 1.45). Cephalothorax light yellow, almost bare, with whitish scales on black anterior edge and around lateral eyes, spots of brown scales behind PLE. Two transverse spots of brown scales at mid-length of posterior thoracic slope, forming a semicircular dark band, broken in the middle; a thin dark ventral line along the edge of carapace, covered with brown scales. Abdomen whitish above, laterally brown with white stripe; lower sides whitish; spinnerets light greyish-yellow. Frontal aspect whitish with edge of eye field dark, covered by sparse whitish scales, clypeus light fawn; anterior eyes surrounded by long colorless setae; clypeus almost bare. Chelicerae whitish-yellow, with transverse dark brown band in proximal ⅓; a brown spot on distal end of pedipalpal femur and an irregular dark grey line along ventro-prolateral edge of femur I. *Legs:* Legs I yellowish-white. Legs II–IV whitish with some segments yellow. No darkenings on legs other than a dark line along anterior surface of femur I. Leg formula 4–3–1–2, patella-tibia III=IV. Patella-tibia I length 1.5–1.7 (x̄ = 1.61). *Palps:* Pedipalps light yellow, with brownish-yellow dorsal surface of tibia and cymbium. Embolus located antero-ventrally, makes 1½ coil; tibial apophysis of medium length, ventrally appears as a narrow plate, rounded apically, laterally tongue-like; tibia short (Figs. 21, 22).

Female: (n = 5). Total length 5.6–6.4 (x̄ = 6.02), length of carapace 2.4–2.7 (x̄ = 2.54), maximum carapace width 1.8–1.9 (x̄ = 1.86), eye field length 1.30–1.35 (x̄ = 1.31), eye row I width 1.65–1.75 (x̄ = 1.68). Body shape and proportions resembling male, pale colored, without contrasts, except dark rims around
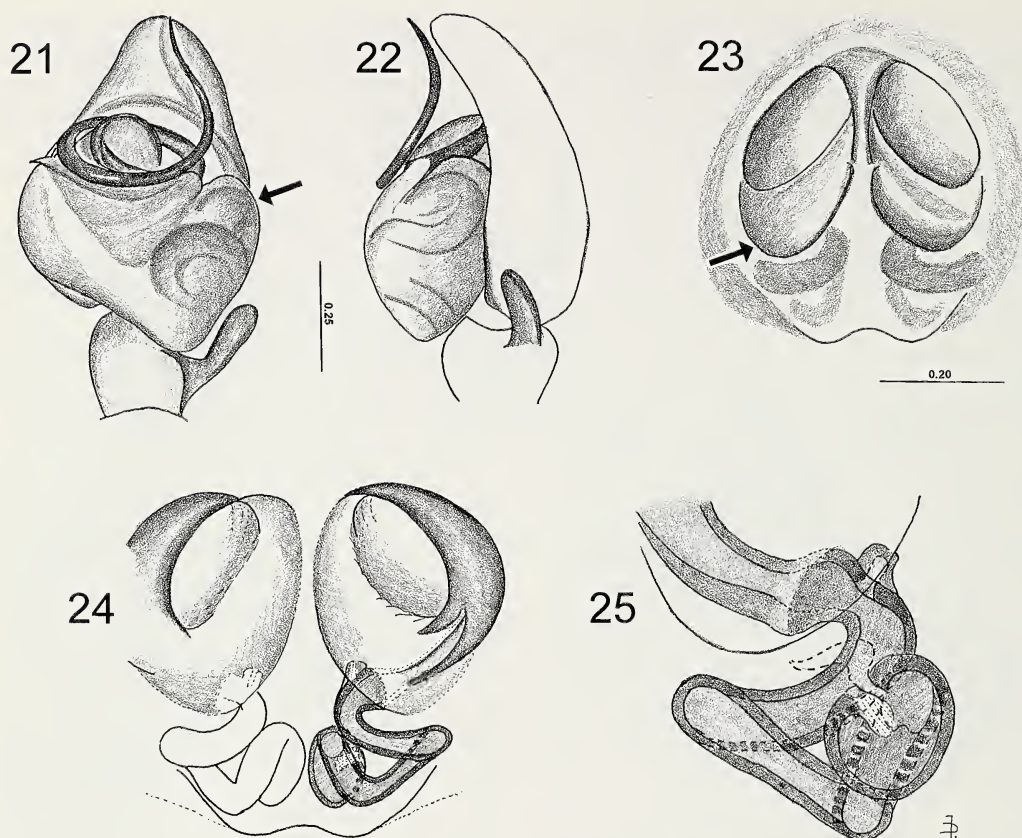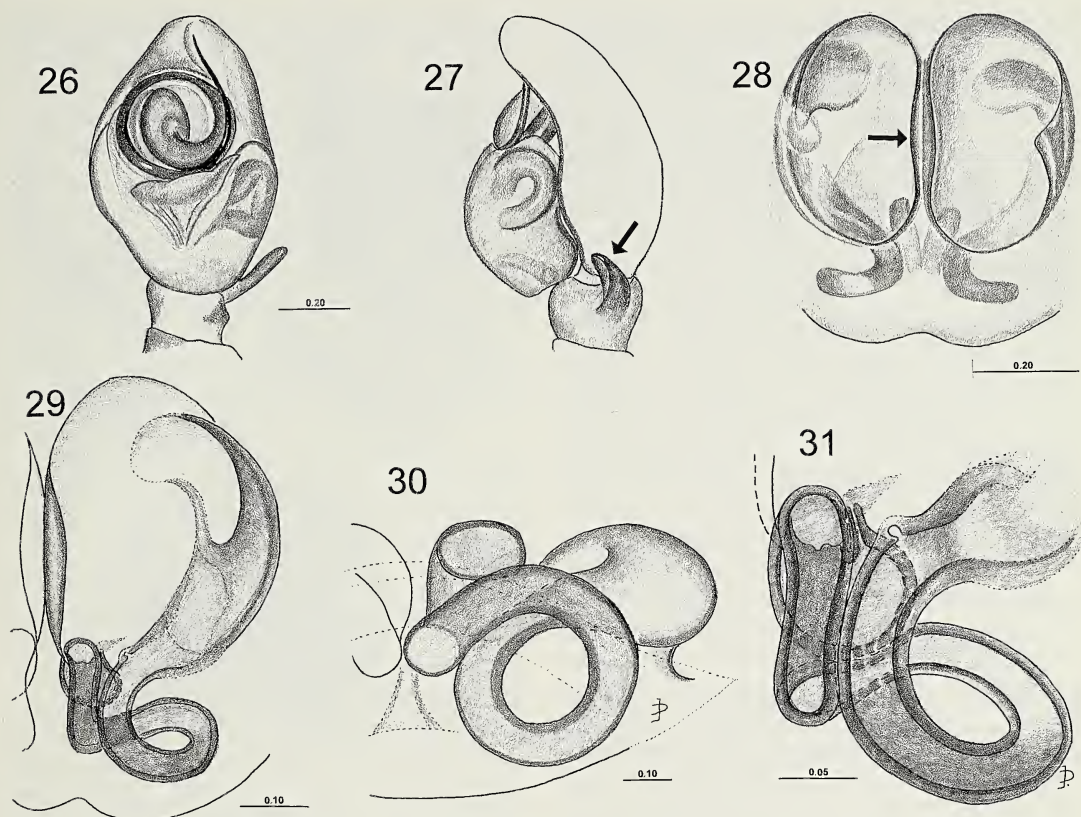
Figures 21–25.—*Cytaea ponapensis* new species from Ponape, Caroline Islands. 21, Palp of holotype ventrally, with arrow indicating plate-like tibial apophysis; 22, Palp of holotype laterally; 23, Epigynum, with arrow showing fossae distinct with obliquely divergent anterior portions; 24, Internal structure of epigynum, ventral view; 25, Spermatheca, dorsal view, left side.

AME and lateral eyes. Cephalothorax yellowish with eye field whitish and with yellowish-grey scales on thoracic region. Abdomen light, covered uniformly with light yellowish-grey scales. Frontal aspect whitish, anterior eyes surrounded with dense long white scales; clypeus very low; chelicerae, pedipalps and leg I whitish to whitish-yellow. *Legs:* Whitish. Leg formula 4–3–1–2, patella-tibia III=IV. Patella-tibia I length 2.0–2.2 ($\bar{x}$ = 2.07). *Epigynum:* (Figs. 23–25). With two large oval fossae, surrounded by thin sclerotized rim; anterior part further depressed and also thinly dark rimmed. These deeper depressions form the entrance to a large chamber-like anterior part of copulatory duct, which runs semicircularly, narrowing, around anterior half of epigynum. At the posterior end of the fossa the copulatory ducts pass through short, non-sclerotized passage into a narrow sclerotized spermatheca. The spermatheca turns laterally, then medially, to an oval, terminal chamber. That structure resembles closely internal structures of epigynum in *Cytaea rai* new species from Yap, and a little less closely *Cytaea carolinensis* new species from Palau.

Material examined.—CAROLINE ISLANDS: *Ponape,* Kolonia, roadside near Cliff Rainbow Hotel, 4♀, 3 June 1973 (JWB & JAB). Palm forest E of Kolonia, elev. 200 ft., 1♀ 3imm, 5 June 1973 (JWB & JAB). Nett Municipality, Nan Pil, about 1500 ft., tree shaking, 3♂1♀ 1imm, 6 June 1973 (JWB & JAB). E of Kolonia, breadfruit-ivory nut palm forest, hand collecting, 2♂, 8 June 1973 (JWB & JAB). SW of Sekere School, shaken from bushes on roadside bank, 1♂1♀, 10 June 1973 (JWB & JAB).

Distribution.—Known only from Ponape, Caroline Islands.

Figures 26–31.—*Cytaea rai* new species from Yap, Caroline Islands. 26, Palp of holotype ventrally; 27, Palp of holotype laterally, with arrow indicating hook-like tibial apophysis; 28, Epigynum, with arrow indicating swelling at mid-length; 29, Internal structure of epigynum showing single spermatheca and ducts; 30, Internal structure of epigynum, posterior view, showing coiling of ducts; 31, Detail of epigynal coils, dorsal view, left side.

Cytaea rai new species
Figs. 26–31, Map 2

Holotype.—Holotype male from Caroline Islands, Yap, Yap I., Fedor, nightlighting in forest, 19 February 1980, (J.W. Berry) (BPBM).

Etymology.—*Rai,* a noun in apposition, are the large stone discs used as money in Yap.

Diagnosis.—The very broad palpal bulb lacking hooks or projections, the embolus coiled flat on the bulb ventrally, and the short, broad curved tibial apophysis of the palp (Figs. 26, 27) distinguish the male from other species of the genus. The female resembles *C. laticeps* (Thorell 1878) and *C. sinuata* (Doleschall 1859), but differs from them by the large oval windows of the epigynum in combination with a swelling at midlength of the septum (Figs. 28, 29).

Description.—*Male: (n = 3).* Total length 4.3–4.8 ($\bar{x}$ = 4.55), length of carapace 2.0–2.3 ($\bar{x}$ = 2.15), maximum carapace width 1.4–1.5 ($\bar{x}$ = 1.48), eye field length 1.1–1.2 ($\bar{x}$ = 1.18), eye row I width 1.45–1.55 ($\bar{x}$ = 1.52). Cephalothorax light yellow, almost bare, with a few whitish scales on black ring of lateral eyes, spots of brown scales behind PLE and two transverse spots of brown scales in the midlength of posterior thoracic slope, making together a semicircular dark band, broken in the middle. A thin dark line along the ventral edge of carapace, covered with brown scales. Abdomen whitish, with a marginal brown streak of scales that connects angularly near spinnerets with a similar lower streak, along the sides, leaving a white streak between the dark ones; lower sides whitish; spinnerets light greyish-yellow. Frontal aspect whitish with eye field and clypeus light brown; anterior eyes surrounded by long setae with whit-

ish ends. Clypeus almost bare. Chelicerae whitish-yellow, with transverse dark brown band in proximal ⅓ of their length. A dark spot on prolateral apical end of palpal femur and an irregular dark grey line along prolateral surface of femur I. Pedipalps light, with darker tibia and light brown dorsal surface of cymbium. *Legs:* Legs I yellowish-white, some segments yellow, with long, brown spines; dark line along anterior surface of femur I. Leg formula 4=3–1–2, patella-tibia III=IV. Patella-tibia I length 1.65–1.75 ($\bar{x}$ = 1.70). *Palp:* Embolus located antero-ventrally, makes 1½ coils; tibial apophysis of medium length, ventrally appears as a narrow plate, rounded apically, laterally hook-like; tibia short (Figs. 26, 27).

Female: (n = 3). Total length 5.2–6.1 ($\bar{x}$ = 5.75), length of carapace 2.0–2.5 ($\bar{x}$ = 2.35), maximum carapace width 1.5–1.8 ($\bar{x}$ = 1.70), eye field length 1.1–1.3 ($\bar{x}$ = 1.25), eye row I width 1.1–1.3 ($\bar{x}$ = 1.25). Body shape and proportions resembling male, pale without striking contrasts. Cephalothorax yellowish with eye field whitish and with colorless scales. Abdomen whitish, no pattern visible. Frontal aspect whitish, the anterior eyes surrounded with dense, long, white scales; clypeus very low; chelicerae, pedipalps and leg I whitish to whitish-yellow. *Legs:* Leg formula 4–3–1=2; patella-tibia III=IV. Patella-tibia I length 1.5–2.0 ($\bar{x}$ = 1.85). *Epigynum:* With two large oval fossae. Septum with a swelling at mid-length (Figs. 28, 29). Duct curving first laterally, then medially and forward to the spermatheca (Figs. 30, 31).

Material examined.—CAROLINE ISLANDS: *Yap,* Fedor Village, nightlighting, 1♂ (holotype), 19 February 1980 (JWB). Fedor Village, Dalipebinau Municipality, coconut grove, tree shaking, 1♂ 1imm, 29 January 1980 (JWB). Gagil-Tomil, mixed forest, 1♂ 1imm, 30 May 1973 (JAB & JWB). Colonia, St. Mary's school, sweeping bushes, 2♀ 3imm, 11 March 1980 (JWB). Aringel village, tree shaking, 1♀ 5imm, 3 March 1980 (JWB).

Distribution.—Known only from Yap Island in the Caroline Islands.

Cytaea vitiensis new species
Figs. 32–35, Map 2

Holotype.—Holotype male from Fiji, Viti Levu, Nausori Highlands Forest Reserve, Koronsingalevu Block, elev. 1500 ft., sweeping
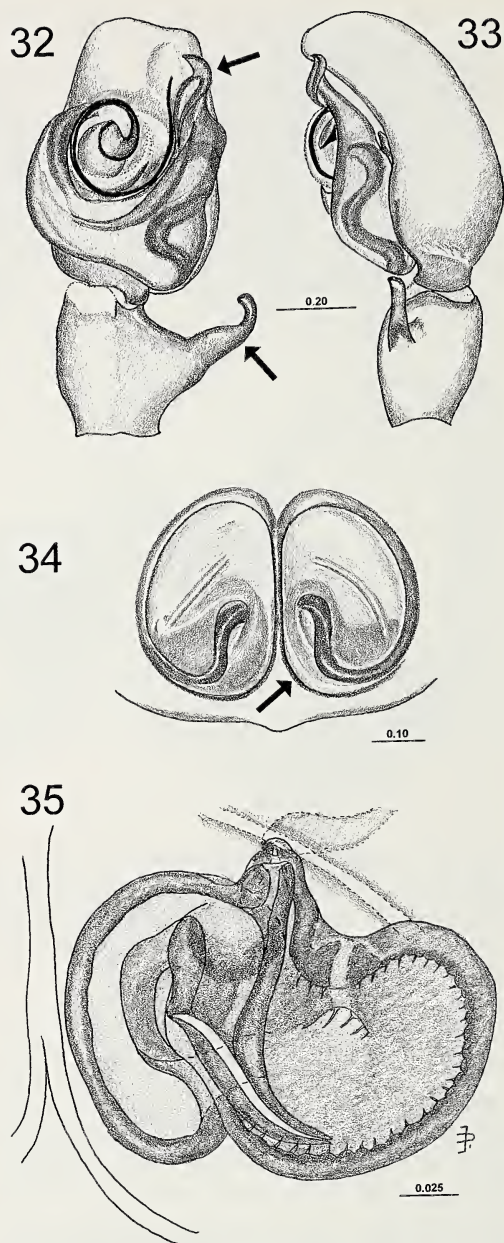
Figures 32–35.—*Cytaea vitiensis* new species from Viti Levu, Fiji. 32, Palp of holotype ventrally, with arrows showing twisted process near distal end of bulb and the strongly curved tibial apophysis; 33, Palp of holotype laterally; 34, Epigynum, showing oval fossae and sclerotized structures distal from septum; 35, Internal structure of epigynum with left spermatheca and ducts.

and shaking, 27 May 1987, (J.W. & E.R. Berry) (BPBM).

Etymology.—Named for its occurrence on the island of Viti Levu, Fiji.

Diagnosis.—Similar to *Cytaea nausori* new species. Epigynum differing by the more oval fossae and the sclerotized structures near opening being more distant from the septum (Figs. 34, 35). In males, palp with retrolateral part of bulb produced distally into a twisted process that extends beyond alveolus nearly to end of cymbium; tibial apophysis strongly curved, set on projection of retrolateral tibia surface (Figs. 32, 33).

Description.—*Male:* (*n* = 5). Total length 5.0–5.5 ($\bar{x}$ = 5.19), length of carapace 2.3–2.6 ($\bar{x}$ = 2.46), maximum carapace width 1.8–1.9 ($\bar{x}$ = 1.85), eye field length 1.3–1.4 ($\bar{x}$ = 1.39), eye row I width 1.7–1.9 ($\bar{x}$ = 1.80). Cephalothorax covered with minute, semi-transparent colorless scales, plus a few light brown scales; eye field light fawn, black pigmented area around lateral eyes covered with whitish scales between anterior eyes and PLE, with reddish-brown scales below PME and behind PLE, intermixed with whitish scales behind the anterior eyes. Cephalothorax light brown dorsally with black rings around eyes, a broad band of dark brown scales running in a "U" below eyes from anterior corners of carapace across thoracic slope. Below and behind the dark band is a marginal band of white scales. Abdomen pale yellowish-brown, with small whitish and brownish scales, forming three pairs of narrow diagonal spots, a pair of white spots anteriorly, and an indistinct white marginal line. Sparse dark setae scattered over the abdomen. Frontal aspect with face light brown, the anterior eyes surrounded by whitish setae dorsally with a few brown ones, ventrally by setae basally dark, apically whitish. Clypeus light brown without contrasting spots or scales; chelicerae slender, short, light brown, covered basally and along retrolateral edge with long whitish setae. Pedipalps with femur whitish with a faint apical annulus, patella greyish-yellow, with tibia and cymbium basally brownish-yellow. *Legs:* Femur I whitish, with apical annulus, remaining segments brownish-yellow, with two indistinct dark brown annuli on tibia I. Legs II-IV whitish-yellow; all spines long. Leg formula 1–4=3–2; patella-tibia III≧IV. Patella-tibia I length

2.0–2.1 ($\bar{x}$ = 2.06). *Palp:* As described in diagnosis (Figs. 32, 33).

Female: (*n* = 1). Total length 6.6, length of carapace 2.7, maximum carapace width 2.0, eye field length 1.3, eye row I width 1.9. Cephalothorax yellow with a lighter diamond-shaped spot behind eye field and lighter on lower sides, transverse band of sparse darker brown scales across median part of posterior thoracic slope. Lateral eyes, on black pigmented spots, are surrounded with whitish scales. Frontal aspect pale yellow without contrasting marks, the anterior eyes surrounded by whitish setae. Abdomen pale, with brownish scales delimiting an indistinct paler triangular area anteriorly and a diamond-shaped one posteriorly. *Legs:* Legs II-IV uniformly whitish, with tibiae-tarsi yellow. Leg formula 4–3–2 (Leg I missing), patella-tibia III≧IV. *Epigynum:* Similar to *Cytaea nausori*, differing as described in diagnosis (Figs. 34, 35).

Material examined.—FIJI: *Viti Levu,* Nausori Highlands Forest Reserve, Koronsigalevu Block, elev. 1500 ft., sweeping, shaking, 1♂ (holotype), 27 May 1987 (JWB & ERB). Nandarivatu, tree shaking, elev. 900 m, 1♂, 1 April 1987 (ERB). Nandarivatu, Koro o' road at microwave tower, sweeping roadside vegetation, 1♀ 1imm, 13 May 1987 (JWB & ERB). Mangrove swamp by road near Namuka Harbor, sweeping, 1♂ 3imm, 2 May 1987 (JWB & ERB). Hill forest about 8 mi NE of Navua, tree sweeping, shaking, 3♂ 4imm, 2 May 1987 (JWB & ERB). Lami, tree in field, 4♂ 7imm, 23 May 1987 (JWB & ERB).

Distribution.—Known only from Viti Levu in Fiji.

Genus *Hasarius* Simon 1871

Type species *Attus Adansonii* Audouin 1825. Location or existence of type specimens is unknown.

Hasarius adansonii (Audouin 1825)

Attus Adansonii Audouin 1825, p.169
Hasarius Adansonii: Simon 1871, p. 330.

Discussion.—This nearly cosmopolitan salticid has numerous synonyms (see Bonnet 1957). It has been described and illustrated frequently (e.g., Davies & Żabka 1989). We present here only new collection records.

Material examined.—PHILIPPINE ISLANDS: *Luzon,* 4♂4♀ 1imm. MARSHALL ISLANDS: *Eniwetok,* 32♂47♀ 63imm. *Majuro,* 2♀. FIJI: *Viti Levu,* 5♂4♀ 4imm. COOK ISLANDS:

Rarotonga, 1♂. **MARQUESAS ISLANDS**: Nuku Hiva, 3♂7♀ 8imm. **HAWAIIAN ISLANDS**: *Hawaii*, 8♂13♀ 13imm; *Midway*, 1♂.

Distribution.—Asia, Africa, North America, South America, Europe, Australia, Oceania.

Genus *Lakarobius* new genus

Type species.—*Lakarobius alboniger* new species, from Viti Levu, Fiji.

Etymology.—*Lakarobius* signifies living in trees, from Greek *lakara*, a kind of tree, and *bios*, life. Gender masculine.

Diagnosis.—Resembles *Cytaea* and *Xenocytaea* in male genitalia; however, the combination of four-cusped retromarginal cheliceral tooth (two cusps in *Cytaea* and *Xenocytaea*), two promarginal cheliceral teeth (4–5 in *Cytaea*), absence of lateral spines on metatarsus I and non ant-like form distinguishes *Lakarobius* from all other Pacific fissident genera.

Descriptive notes.—Small black and white fissident salticid genus. Chelicerae with four-cusped retromarginal cheliceral tooth and two promarginal cheliceral teeth. With patellar spines. Without lateral spines on tibiae and metatarsi I and II. With 3–3 ventral spines on tibiae I and II, 2–2 ventral on metatarsi I and II. With 3 to 5 dorsal spines on each femur.

Lakarobius alboniger new species
Figs. 36–43

Holotype.—Holotype male from Fiji, Viti Levu, Nausori Road, 3 km N of Queen's Road, tree shaking in forest, 7 May 1987 (J.W. Berry, E.R. Berry and J.A. Beatty) (BPBM).

Etymology.—The specific name *alboniger*, "white-black", refers to the conspicuous black and white dorsal pattern of the spider.

Diagnosis.—In addition to the generic characters, the color pattern, long straight proximal lobe on the male palpal bulb, sinuous tibial apophysis of the male palp, and epigynal structure distinguish the single species of this genus from all other known Pacific salticids (Figs. 36–38).

Description.—*Male*: ($n = 5$). Total length 2.9–3.3 ($\bar{x} = 3.01$), length of carapace 1.3–1.4 ($\bar{x} = 1.36$), maximum carapace width 1.00–1.03 ($\bar{x} = 1.02$), eye field length 0.8–0.9 ($\bar{x} = 0.87$), eye row I width 1.00–1.03 ($\bar{x} = 1.02$). Cephalothorax with greyish-brown eye field, black around lateral eyes and dark brown belt running below lateral eyes and around thoracic slope, leaving large white spot on flat surface of cephalothorax behind eye field. A white belt along lower sides and lower thoracic slope, the ventral margin of cephalothorax dark. Eye field covered with minute adpressed setae. Abdomen with large blackish and white areas (Figs. 36, 37) covered with sparse minute setae. Frontal view with face so reduced that prominent AME take all its width, ALE protruding from lateral surfaces, height of clypeus equal to ¼ of AME's diameter. Face brown, with sides covered with fine whitish setae; clypeus mostly bare, brown, with a row of long whitish setae. Chelicerae short, about AME's diameter, with slight basal bulge; white, with small dark spot on bulge. Anterior eyes surrounded with whitish setae; with ALE slightly above AMEs, their diameter equal to ½ that of AME. Pedipalps whitish, tibia and cymbium dorsally brownish, and patella grey at apex. *Legs:* Legs I white with thin grey line along prolateral surfaces of femur, patella, tibia and tarsus; faint traces of such lines prolaterally on tibiae II–IV. Leg formula 1=4–2–3, patella-tibia III>IV. Patella-tibia I length 1.1–1.2 ($\bar{x} = 1.14$). *Palp:* Reservoir sinuous, a broad coil of embolus in ventral plane, bulb broad with posterior extension over anterior part of tibia, tibia short, tibial apophysis of medium length, narrow, slightly sinuous (Figs. 41–43).

Female: ($n = 5$). Total length 3.1–3.4 ($\bar{x} = 3.28$), length of carapace 1.2–1.4 ($\bar{x} = 1.33$), maximum carapace width 1.0–1.1 ($\bar{x} = 1.05$), eye field length 0.8–0.9 ($\bar{x} = 0.86$), eye row I width 1.00–1.03 ($\bar{x} = 1.01$). Differs from male by lighter brown coloration of face; pedipalps white. Ventral view generally whitish with mouth parts slightly darker, abdomen in part suffused yellowish-grey (Fig. 38). *Legs:* Long and thin. Dark line on prolateral surfaces of leg I reduced to short black lines apically on femur, basally on patella and apically on tibia; weaker blackish spots retrolaterally on patella and tibia. Other legs entirely whitish with exception of small black spots on patella and tibia IV. Leg formula 1=4–2–3; patella-tibia III=IV. Patella-tibia I length 1.2–1.3 ($\bar{x} = 1.21$). *Epigynum:* With two oval membranous windows, with spherical spermathecae located posterior to windows; copulatory openings invisible externally, (observable under compound microscope after staining with
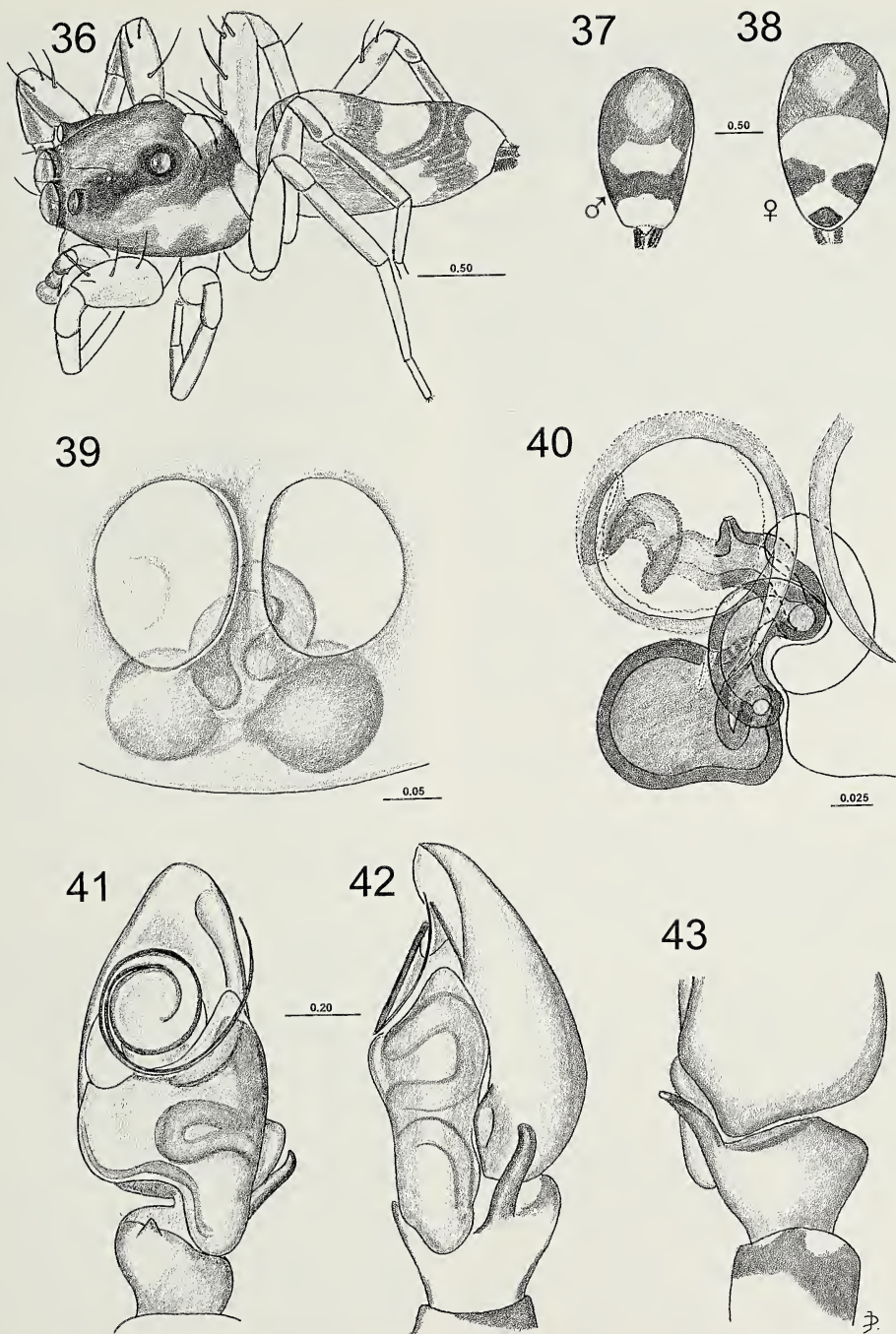
Figures 36–43.—***Lakarobius alboniger*** new species from Viti Levu, Fiji. 36, Holotype male, general appearance; 37, Holotype male, abdominal pattern; 38, Female abdominal pattern; 39, Epigynum; 40, Internal structure of epigynum, right spermatheca and ducts; 41, Palp of holotype ventrally, with arrow indicating posterior extension of bulb; 42, Palp of holotype laterally; 43, Holotype pedipalpal tibia, dorsally.

Chlorazole Black E), located on lateral margin
of each window with soft membranous duct
running across window, making three coils
before passing into sclerotized duct, which
runs axially and makes two coils before open-
ing to spermatheca (Figs. 39, 40).

Material examined.—FIJI: *Viti Levu,* Lami on
tree in field, 2♂1♀, 23 May 1987 (JWB & ERB).
Suva, Lauthala Bay, mangrove, 1♀, 29 May 1987
(JWB & ERB). Near Namuka Harbor, mangrove
swamp by road, sweeping, 2♂3♀ 2imm, 2 May
1987 (JWB & ERB). Near Namuka Harbor, on
mangrove, 1♂ 1imm, 2 May 1987 (JWB & ERB).
Namosi Road, 7.7 km N of Queen's Road, roadside
sweeping & shaking, 1♂, 7 May 1987 (JWB &
ERB). Namosi Road, 3 km N of Queen's Road, tree
shaking in forest, 5♂ (including holotype) 6♀
9imm, 7 May 1987 (JAB, JWB & ERB). 8 mi NE
of Navua, tree shaking, 1♂ 1imm, 2 May 1987
(JWB & ERB). 8–10 mi N of Nausori, hill forest,
1♂, 19 May 1980 (JWB & ERB). Nanduruloulou
Research Stat., about 5 mi W of Nausori, shaken
from dead banana leaves, 1♀, 15 May 1987 (JWB
& ERB). Namosi Road, 7.7 km N of Nausori, on
vegetation, hill forest, 1♂, 19 May 1987 (JWB &
ERB).

Distribution.—Known only from Viti
Levu, Fiji.

Genus *Menemerus* Simon 1868

Type species *Attus semilimbatus* Hahn 1827, p. 5.
Location or existence of type specimens is un-
known.

Menemerus bivittatus (DuFour 1831)

Salticus bivittatus DuFour 1831, p. 369.
Menemerus bivittatus (DuFour): Simon 1901, p.
599.

Discussion.—A cosmotropical salticid with
many synonyms (see Bonnet 1957). Recently
illustrated by Davies & Żabka (1989). We
present only new collection records.

Material examined.—MARSHALL IS-
LANDS: *Kwajalein,* 3♀ 5imm; *Majuro,* 4♂4♀
8imm; **MARIANA ISLANDS:** *Guam,* 1♀ 3imm.
CAROLINE ISLANDS: *Palau,* 16♂13♀ 6imm;
Yap, 2♂3♀ 2imm; *Truk,* 1♂; *Ponape,* 1♂1♀ 3imm.
FIJI: *Viti Levu,* 2♂1♀. **COOK ISLANDS:** *Raro-
tonga,* 2♂; *Aitutaki,* 1♂1♀. **SOCIETY ISLANDS:**
Moorea, 1♂5♀ 2imm. **TUAMOTU ISLANDS:**
Manihi, 2♀ 1imm; *Rangiroa,* 1♀. **MARQUESAS
ISLANDS:** Nuku Hiva, 2♂ 5imm. **HAWAIIAN
ISLANDS:** *Midway,* 3♀.

Distribution.—Cosmotropical.

Map 3.—Distribution of three species of *Pseu-
dicius* in the Pacific. *Pseudicius kraussi* (●), *Pseu-
dicius punctatus* (○), and *Pseudicius nuclearis* (★).

Genus *Pseudicius* Simon 1885

Type species *Aranea encarpata* Walckenaer 1802,
p. 241. Location of type specimen unknown.
Pseudicius Simon 1885a, p. 28.
Afraflacilla Berland & Millot 1941, p. 328 (syn-
onymized with *Pseudicius* by Clark 1974, p.
22; removed from synonymy by Żabka 1993,
p. 280).
Savaiia Marples 1957, p. 388 (first synonymized by
Prószyński 1990, p. 316).

Discussion.—A diverse unident genus,
containing more than 60 species spread over
Europe, Africa, Asia, Australia and Pacific is-
lands, which presents formidable difficulty in
interpretation of relationships among species
and groups of species. The problems it poses
have been discussed on several occasions,
most recently in Prószyński 1992.

Since that time Żabka (1993) proposed the
transfer of about 40 species (without listing
them) to a separate genus under the junior
synonym *Afraflacilla* Berland & Millot 1941.
Żabka acknowledges that *Pseudicius* is the
closest relative of *Afraflacilla* because "both
have similar habitus, femoral and carapace tu-
bercles and homologies in palpal organ struc-
tures." However, species illustrated in his pa-
per show characteristic traits visible in various
groups of *Pseudicius,* like a frequently bira-
mous tibial apophysis, but in some species
with reduction or loss of either ramus, in-
crease in length of embolus, from a very short
apical one to twisting around bulb. Other vari-

able characters include presence or absence of distinctive epigynal pockets and various length of copulatory ducts, often coiled in various ways. Separation of *Afraflacilla* from the remaining *Pseudicius* would cut across relationships and complicate phyletic and zoogeographic patterns of the genus, without really contributing to our understanding of the relationships within the genus.

Diagnosis.—An elongate rather flattened unident salticid with a row of spine-bearing tubercles below the eyes and a row of microspines on femur I. This presumed stridulatory apparatus (Maddison 1987) is not present in any other genus in the geographical area considered here.

Description.—With a stridulatory row of tubercles with spines beneath the lateral eyes (Figs. 44–46), corresponding with a row of microspines on tubercles on the prolateral surface of femur I, visible only under very high magnification. Body very characteristic: elongated and relatively flat, with long, low cephalothorax, and long, low narrow abdomen. Legs I elongated and robust, heavily sclerotized, with swollen tibia and femur and reduced spines; remaining legs slender and shorter; however, in females legs IV are the longest. Abdomen elongate oval, posteriorly pointed, with a characteristic pattern, common to a majority of species. Chelicerae short and proportionally broad, slightly bulging, with one retromarginal and two promarginal teeth. *Palp:* Relatively simple, frequently with biramous tibial apophysis, but varying by enlargement or reduction (in some cases complete loss) of either ramus. Length of copulatory ducts in females seems to correlate with length of embolus in males. Epigynum usually with a pair of external pockets of various shape, located in various parts of the epigynum, missing in some species. In spite of differences in male and female genital organs, these structures show a number of similarities and can be arranged into morphoclines, connecting seemingly very different forms.

Pseudicius kraussi (Marples)
Figs. 44–52, 57, 58; Map 3

Flacilla kraussi Marples 1964, p. 405, fig. 5.
*Flacillula kraussi*: Brignoli 1983, p. 638.
Pseudicius samoaensis Prószyński 1992, p. 110–111, figs. 117–120 (NEW SYNONYMY).

Discussion.—Until now, *Pseudicius kraus-*

si has been known only from male specimens and *P. punctatus* (Marples 1957) only from females (see following species). With some doubt we assign a single female specimen from Eniwetok (Marshall Islands) to *P. kraussi*. The epigynal differences between this specimen and *P. punctatus* are relatively small, however; and the two species may be synonymous. We have too few specimens from any one locality to reveal the amount of epigynal variability. The other species of *Pseudicius* known from Eniwetok, *P. nuclearis* Prószyński 1992, is quite different from *P. kraussi* and *P. punctatus* in both sexes. *Pseudicius samoaensis* Prószyński 1992 agrees with *P. kraussi* in all characters. Marples's misplacement of *kraussi* in *Flacilla* is probably the reason for the description as a separate species by Prószyński.

Description.—*Male: (n = 5).* Total length 3.7–5.3 (x̄ = 4.71), length of carapace 1.6–2.2 (x̄ = 2.02), maximum carapace width 1.1–1.6 (x̄ = 1.34), eye field length 0.8–1.1 (x̄ = 0.97), eye row I width 0.9–1.1 (x̄ = 1.03). Cephalothorax brown with darker eye field, median spot of white setae on anterior thoracic region, indistinct band of white setae along ventral margins of carapace. A row of 12 stridulatory spines on tubercles under lateral eyes (Fig. 46). Abdomen elongate oval, pale, with indistinct pattern of brownish spots, an indistinct marginal line of whitish setae (Fig. 51). Frontal aspect, clypeus very low, with a row of tiny, almost invisible colorless setae; chelicerae somewhat elongate, brown. *Legs:* Legs I long and robust, brown. Femur I with a compact row of five stridulatory tubercles with microspines, and two more distant, one distally, one above; tibia I brown, with single reduced spine prolaterally, a mid-ventral row of two minute papillate spines (Figs. 57, 58); remaining legs greyish-yellow, short and slender. Leg formula 1–4–3–2; patella-tibia III<IV. Patella-tibia I length 1.3–2.6 (x̄ = 2.03). *Palp:* Of the *P. tamaricis* (Simon 1885b) type, from which *P. kraussi* differs in longer bulb and embolus, the latter more curved, also tibial apophysis is more curved (Figs. 47, 48) (*cf.* Prószyński 1987:52). Differs from *P. reiskindi* Prószyński 1992 in broader bulb, tibial apophysis longer, straighter, apically slightly hooked (Fig. 48).

Female: (n = 1). Total length 4.8, length of carapace 2.1, maximum carapace width 1.5,
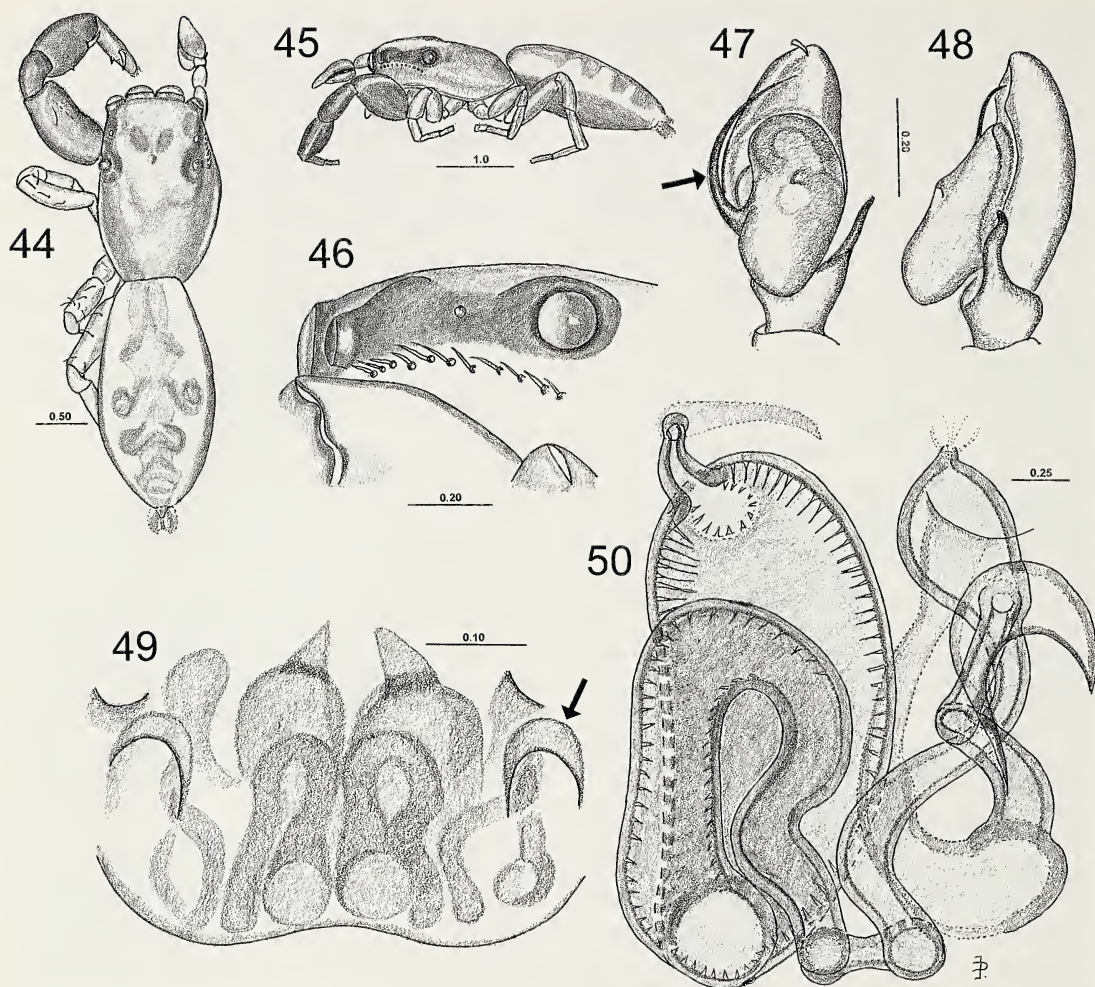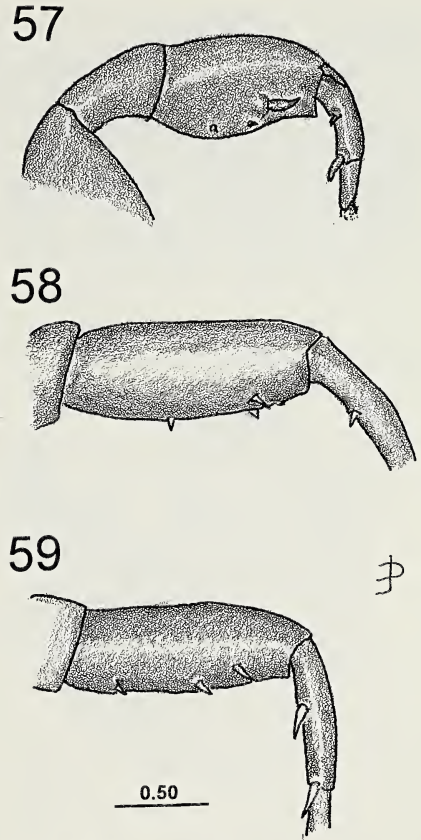
Figures 44–50.—*Pseudicius kraussi,* holotype male from Aitutaki, Cook Islands; female from Eniwetok, Marshall Islands. 44, Dorsal view of male; 45, Lateral view of male; 46, Lateral eyes and row of spines on papillae; 47, Palp ventrally, with arrow indicating embolus; 48, Palp laterally; 49, Epigynum, with arrow indicating anteriorly-placed sclerotized pocket; 50, Internal structure of epigynum, left single spermatheca and ducts.

eye field length 1.0, eye row I width 1.1. Virtually identical to male, except as follows: carapace and leg I lighter brown, dorsum of abdomen without brown median stripe, instead whitish flanked by broad V-shaped band crossed at middle of length and more posteriorly by narrow transverse white setal bands (Fig. 52). *Legs:* Leg I less robust than in male with only one ventral spine on tibia of right leg. Left leg I regenerated, smaller and without spines. Leg formula 4–1–3–2, patella-tibia III<IV. Patella-tibia I length 1.6. *Epigynum:* (Figs. 49, 50). Closely resembles that of *P. punctatus* but has sclerotized pockets placed more anteriorly (Figs. 49, 60).

Material examined.—COOK ISLANDS: *Aitutaki,* 1♂, *Flacilla kraussi* Marples (holotype), No. 10,211, 1961 (N.L.H. Krauss) (BPBM). **SAMOA**: *Mo'ata* near Apia, from mangroves, 18 March 1962 (R.W. Taylor), 1♂ (holotype), *Pseudicius samoaensis* Prószyński 1992 (MCZ). **MARSHALL ISLANDS**: *Eniwetok Atoll,* Libiron Islet, *Pisonia* forest, shaken from trees, 1♀ 7imm, 21 June 1969 (JWB). Libiron Islet, *Pisonia* forest, picked off trees, 1♂, 21 June 1969 (JWB). Japtan Islet, *Pisonia* forest, shaken from trees, 1♂, 30 June 1969 (JWB). Buganegan Islet, mixed forest, beaten onto sheet, 2♂ 3imm, 6 August 1969 (JWB). *Majuro Atoll,* Majuro Islet, coconut/breadfruit, shaken from trees, 1♂ 1imm, 2 August 1969 (JWB).

1.0
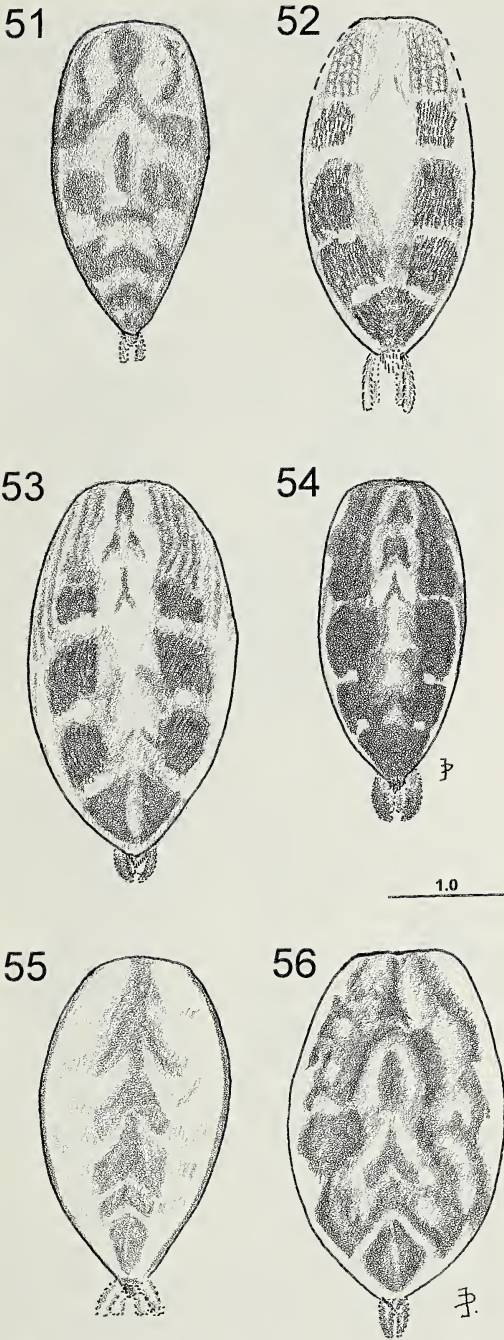
Figures 51–56.—Variation in abdominal pattern in Pacific species of *Pseudicius*. 51, *Pseudicius kraussi* holotype male from Aitutaki, Cook Islands; 52, *Pseudicius kraussi* female from Eniwetok, Marshall Islands; 53, *Pseudicius punctatus* female from Viti Levu, Fiji; 54, *Pseudicius punctatus* female from Viti Levu, Fiji; 55, *Pseudicius nuclearis* female from Kwajalein, Marshall Islands; 56, *Pseudicius nuclearis* female from Eniwetok, Marshall Islands. All drawings to same scale.

0.50

Figures 57–59.—Comparison of Leg I in males of Pacific species of *Pseudicius*. Note swelling of tibia and reduction of spines. 57, *Pseudicius kraussi* from Majuro (Marshall Islands); 58, *Pseudicius kraussi* holotype from Aitutaki, Cook Islands; 59, *Pseudicius nuclearis* from Kwajalein (Marshall Islands).

Distribution.—Marshall Islands, Cook Islands, and Samoa.

Pseudicius punctatus (Marples 1957)
Figs. 53, 54, 60, 61; Map 3

Savaiia punctata Marples 1957, p. 388.
Pseudicius punctatus: Prószyński 1990, p. 316.

Discussion.—Our specimens are externally similar to the holotype, but a little smaller. Epigynum of the holotype is larger and has longer narrow part of the copulatory duct, making an additional coil between branching to the accessory gland opening and the loop of the broader part (Fig. 61).

Description.—*Female:* (n = 4). Total length 3.7–5.0 ($\bar{x}$ = 4.47), length of carapace
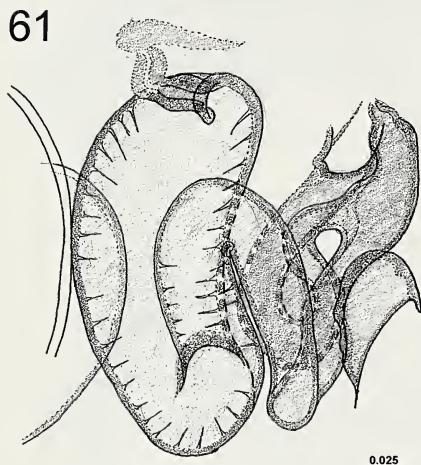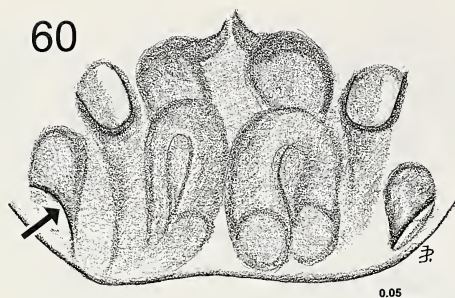
Figures 60–61.—*Pseudicius punctatus* from Viti Levu, Fiji. 60, Epigynum, with arrow indicating postero-lateral pockets; 61, Internal structure of epigynum, with left spermatheca and ducts.

1.7–1.9 ($\bar{x}$ = 1.85), maximum carapace width 1.1–1.3 ($\bar{x}$ = 1.23), eye field length 0.8–0.9 ($\bar{x}$ = 0.86), eye row I width 0.9–1.0 ($\bar{x}$ = 0.99). Cephalothorax dorsally greyish-brown, with median thoracic streak and lower sides much lighter, yellow. Eye field medially darker, covered with delicate whitish adpressed setae; sides yellow, with indistinct, adpressed whitish setae. Ventral edge of carapace dark grey. The characteristic, lateral subocular row of stout setae on tubercles consists of 13 setae. Abdomen whitish-yellow with two broad, dark brown streaks, divided by light lines and white spots into three pairs of dark rectangular spots; there is also a single posterior dark, diamond-shaped spot. Median light streak split anteriorly by thin dark marks. Marginal whitish streaks with sparse reddish-brown setae, lower sides pigmented greyish-yellow, anteriorly and posteriorly suffused

grey. Antero-lateral edges of abdomen with grey lines separated by chains of light spots. Frontal aspect with anterior eyes surrounded ventrally and laterally with white setae, dorsally with finer inconspicuous fawn setae; clypeus with longer white setae. Chelicerae yellow, with a vertical median line suffused grey. Pedipalps pale yellow with long white sparse setae. Ventral aspect light whitish-yellow, sternum with grey margin, abdomen whitish. *Legs:* Legs I yellow, tibia-tarsus I fawn; tibia I with single reduced prolateral spine (rarely two); no retrolateral spines. Leg formula 4–1–3–2, patella-tibia III<IV. Patella-tibia I length 1.0–1.1 ($\bar{x}$ = 1.07). *Epigynum:* Indistinct sclerotized plate with inconspicuous copulatory openings located antero-laterally, and a pair of sclerotized pockets, located postero-laterally (Fig. 60); large coils of spermathecae and parts of ducts are visible through the translucent cuticle. Spermathecae large, vesicular; posterior loop of ducts almost as long as spermatheca itself (Fig. 61).

Male: The male is unknown.

Material examined.—FIJI: *Viti Levu,* Lauthala Bay, mangrove, 3♀, 29 May 1987 (JWB & ERB). **SAMOA:** *Savaii,* 1♀, *Savaiia punctata* (holotype), (Krauss) (BPBM). **CAROLINE ISLANDS:** *Palau,* Malakal, grassy field, 1♀, 17 April 1973 (JAB & JWB).

Distribution.—Known only from Fiji, Samoa, and from Palau in the Caroline Islands.

Pseudicius nuclearis Prószyński 1992
Figs. 55, 56, 59, 62–66, Map 3

Discussion.—This species has been found only on atolls with a strand-type flora and a fauna that is relatively depauperate. The female is here described for the first time.

Description.—*Male:* (*n* = 1). Total length 5.3, length of carapace 2.3, maximum carapace width 1.6, eye field length 1.0, eye row I width 1.3. Cephalothorax brown, white along ventral edge, with small whitish setae on eye field and making median streaks on thoracic region; sides with brown setae, 10 spines below lateral eyes. Face brown with narrow clypeus, edged with short stout white setae; setae around the anterior eyes dorsally white, laterally indistinct fawn. Abdomen whitish with brown median streak, flanked anteriorly by a pair of white spots, slightly expanded medially, sides light brown. Ventral
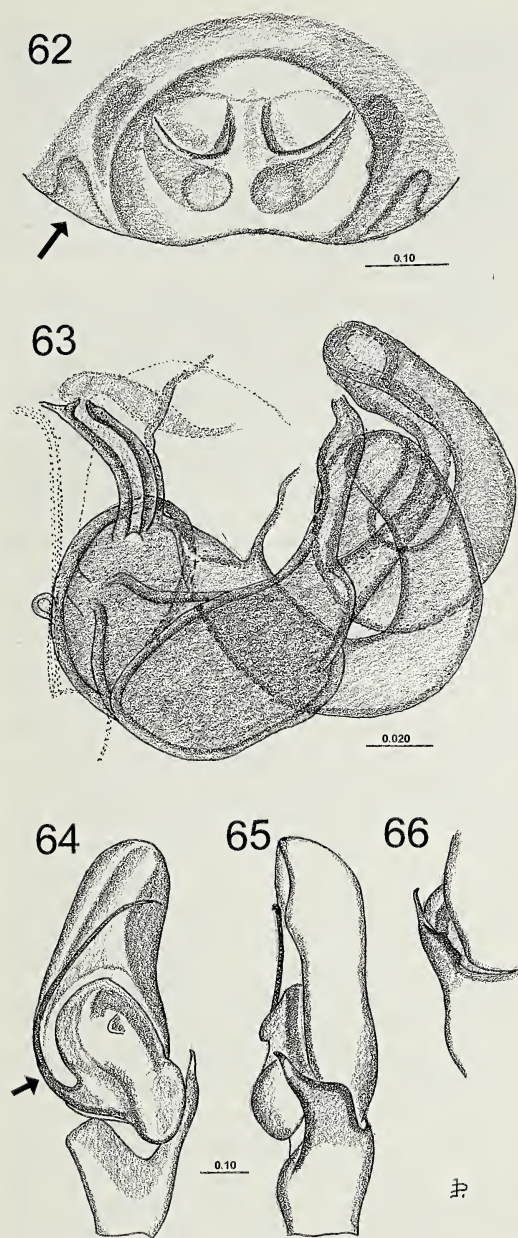
aspect light brown, abdomen light greyish-brown. *Legs:* Legs I more robust and brown, remaining legs yellow, tibia I long, slightly swollen in the posterior half. Ventral spines reduced, three prolateral, one retrolateral in basal position (Fig. 59). Pedipalps yellow, with long white setae on tibia and patella, femur with dorsal white setae apically. Leg formula 1–4–3–2, patella-tibia III<IV. Patella-tibia I length 2.0. *Palp:* (Figs. 64–66). Dorsal ramus straight dorsally ending in a pronounced angle. Bulb oval, set a little diagonally, with slightly expanded basal part, embolus arising at the 8 o'clock position, and running laterally along bulb and extending anteriorly to it about ½ of the bulb length. With long white setae laterally on tibia, dorsally on tibia and proximal half of cymbium.

Female: (*n* = 5). Total length 4.5–6.1 ($\bar{x}$ = 5.37), length of carapace 2.0–2.3 ($\bar{x}$ = 2.18), maximum carapace width 1.5–1.7 ($\bar{x}$ = 1.55), eye field length 0.9–1.1 ($\bar{x}$ = 1.03), eye row I width 1.2–1.4 ($\bar{x}$ = 1.27). Color pattern as in male, but lighter brown. Dorsal stripe narrower than in male, not darker than other dorsal markings. Abdominal pattern (Figs. 55, 56) more diffuse and indistinct in egg-laden specimens. *Legs:* Leg formula 4–1–3–2, patella-tibia III<IV. Patella-tibia I length 1.4–1.6 ($\bar{x}$ = 1.44). *Epigynum:* An indistinct shallow, oval depression with two anterior grooves, relatively deep, separated by a broad ridge (Fig. 62); two posterior pockets, relatively long; resembles *Pseudicius courti* (Żabka 1993) (figs. 5b, c), from which it differs by longer pockets and narrower ridge, longer posterior rim of the grooves. Internal structures, visible through weakly sclerotized cuticle, consist of the copulatory duct running from the copulatory opening dorsally to spermatheca, then making two coils around its posterior part, the bend of the last coil is moved far anteriorly (Fig. 63).

Material examined.—MARSHALL ISLANDS: *Kwajalein Atoll,* Ennylabegan Islet, beach rubble, 1♂ 1imm, 7 July 1969 (JWB); Ennylabegan Islet, on building, 1♀, 25 July 1969 (JWB). *Eniwetok,* Rigili I., clearing in *Pisonia* forest, 1♀, 2 July 1968 (JWB); Buganegan Islet, in *Scaveola* twigs, 1♀, 6 August 1968 (JAB & JWB); Igurin Is., 1♀, 18 July 1968. **CAROLINE ISLANDS:** *Ulithi,* Falalop, coconut forest, litter, 1♀, 2 May 1980 (JWB).

Figures 62–66.—*Pseudicius nuclearis,* female from Eniwetok, male from Kwajalein, Marshall Islands. 62, Epigynum, with arrow indicating posterior pockets; 63, Internal structure of epigynum, with right spermatheca and ducts; 64, Palp ventrally, with arrow showing embolus arising at 8 o'clock position; 65, Palp laterally; 66, Tibial apophysis antero-dorsally.

Map 4.—Distribution of seven species of *Sobasina* in the Pacific. *Sobasina aspinosa* new species (♦), *Sobasina coriacea* new species (■), *Sobasina cutleri* new species (●), *Sobasina platypoda* new species (○), *Sobasina magna* new species (□), *Sobasina paradoxa* new species (☆) and *Sobasina yapensis* new species (★).

Distribution.—Known only from the Marshall Islands and the Caroline Islands.

Genus *Sobasina* Simon 1897
Map 4

Type species *Sobasina amoenula* Simon 1897, p. 297, from Solomon Islands, Vanikoro; in MNHN, Paris.

Discussion.—The genus, first described by Simon in 1897, was based on the single species *S. amoenula*; but Wanless (1978) has been the major contributor to it, adding five species. The present study describes seven new species and gives data on geographic distribution. There are striking differences in development and spination of tibia I: in one species elongate and thin, without any spines; in another with spines limited to anterior half of tibia; in the majority of species with 3–6 ventral spines in each of two rows, evenly distributed along either a cylindrical, narrow tibia, or one that is compressed and expanded ventrally into a semicircular plate-like segment, which has a thin brush of dark, long, flattened setae. Species with ventral setae have the dorsal surface of tibia I broadened. It is peculiar that a similarly semicircular compressed tibia I, with a similar brush of long, flattened setae, occurs in a species of *Efate*, found on the same island (Viti Levu, Fiji). The

number of ventral spines in the rows on tibia I varies in different species from 2–6, to none in *Sobasina aspinosa* new species, where the segment is very long and thin. *Sobasina magna* new species is much larger than the remaining species, is much broader, and may not be an ant mimic. All of this makes the genus an exciting object for comparative studies in many aspects.

Diagnosis.—Ant-like (except *S. magna*), fissident salticids of small to medium size. The only other fissident ant mimics in the Pacific are *Efate* Berland 1938 and *Rarahu* Berland 1929. *Rarahu* differs from *Sobasina* by having leg spines on metatarsus I and none elsewhere. *Efate* differs in the male by the meandering sperm reservoir of the palp (reservoir making a simple circuit around the bulb in *Sobasina* (see Fig. 71)). In the female, *Sobasina* has long spermathecae (Fig. 70) and usually an indistinct epigynum (Fig. 69). The spermathecae of *Efate* are short and the epigynum distinct, with a median posterior arch or emargination. The carapace of the female *Sobasina* also has humps and depressions.

Descriptive notes.—Small to medium size, usually ant-like, fissident jumping spiders, appearing smaller than they are, because of the narrowness of the body, low cephalothorax and slender legs. Cephalothorax flat; females but not males with a constriction just behind the eyes. Cephalothorax strongly sclerotized and shiny, covered densely with small, hemispherical warts. A scutum may cover all or part of the abdominal dorsum. Setae sparse and inconspicuous, except for a ventral brush on tibia I in some species; there are conspicuous dense setae ventrolaterally on last segment of pedipalps in both sexes of some species. Abdominal constriction accentuated in some species by a white ring, line or spot. Thoracic constriction and/or slope in some species lighter, sometimes with a few short white setae. Face usually without contrasting marks, anterior eyes in a straight line, diameter of AME twice that of ALE, clypeus very low. Chelicerae small (except *S. magna*), with one bicusp retromarginal tooth and two promarginal teeth (*S. magna* has an additional retromarginal tooth). Distal segments of female pedipalp flattened, tarsus broadened with a prolateral fringe of dark setae. Palpal bulb a simple oval, with very short apical embolus and simple loop of sperm reservoir duct, tibial

apophysis simple, single, about half length of the bulb or less. Epigynum very small, its internal structure peculiar because of the presence of a chain of small chambers or a thick walled, duct-like structure, which apparently is a modified spermatheca.

KEY TO SPECIES OF *SOBASINA* SIMON 1897
### (expanded from Wanless (1978))

1. Tibia I with dense ventral fringe of flattened black setae (Fig. 75); ventral spines 3–5 in outer row, 1–4 in inner row. 2
   Tibia I without ventral fringe of setae (Fig. 68), ventral spination variable. 5
2. Tibia I short and thick (length only twice depth), flat-topped, with distinct angle between dorsal and lateral surface (Fig. 75). Fiji. . . . . *platypoda* new species
   Tibia length more than twice depth, not flattened or angular 3
3. Eye region finely rugulose anteriorly to granulate posteriorly; thoracic sides granulate. Only male known. Solomon Islands: Rennell . . . . *hutuna* Wanless
   Eye region granulate; thoracic sides irregularly punctured 4
4. Thoracic hump high (Wanless 1978, fig. 3D); thoracic punctures very numerous. New Hebrides (=Vanuatu): Tanna, Efate, Espiritu Santo . . . . *tanna* Wanless
   Thoracic hump low (Wanless 1978, fig. 3B); thoracic punctures less numerous. Solomon Islands: Guadalcanal . . . . *solomonensis* Wanless
5. Ventral spines of tibia I absent or in two rows of 2–3 spines each in distal half of tibia (Wanless 1978, fig. 3C). 6
   Ventral spines of tibia I in two rows of 3–6 spines each, occupying most of tibial length 8
6. Tibia I without ventral spines. Fiji. . . . . *aspinosa* new species
   Tibia I with 2–2 to 2–3 ventral spines in distal half 7
7. Abdomen with dorsal and ventral scuta (Wanless 1978, fig. 7B); chelicerae apparently normal, total length 3.24 mm. Only male known. Bismarck Archipelago . . . . *scutata* Wanless
   Abdomen without scuta; chelicerae slightly concave anteriorly, carinate laterally (Fig. 93), with one promarginal tooth greatly enlarged; length 7.0 mm. Only female known. Tonga . . . . . .
   . . . . *magna* new species
8. Eye region with conspicuous punctures (Wanless 1978, plate 1e). 9
   Eye region without conspicuous punctures, rugulose to granulate. Length 2.0–3.7 10
9. Only eye region and sides of thoracic region conspicuously punctate; length 3.1–5.0 mm (mostly 3.9–5.0). Fiji. . . . . *cutleri* new species
   Entire carapace conspicuously punctate; length 2.1–3.0 mm; Fiji. . . . . *paradoxa* new species
10. Eye region rugulose anteriorly, granulate posteriorly. Only female known. Solomon Islands: San Cristobal (Makira) and Vanikoro. . . . . *amoenula* Simon
    Eye region granulate (Wanless 1978, plate 1a). 11
11. Clypeus densely white-haired. Only male known. Solomon Islands: Kolombangara . . . .
    . . . . *alboclypea* Wanless
    Clypeus not white-haired. 12
12. With a dark prolateral stripe on patella and tibia I. Female abdomen slightly constricted with a single incomplete transverse white band at the constriction (Fig. 67). Male with dorsal abdominal scutum partly divided at the abdominal constriction. Caroline Islands: Yap . . . .
    . . . . *yapensis* new species
    No dark prolateral stripe on patella and tibia I. Female abdomen markedly constricted with two transverse white bands, one at the constriction, one further forward (Fig. 81). Male abdomen unconstricted, the scutum undivided (Fig. 80). Caroline Islands: Palau. . . . . . . *coriacea* new species

Sobasina yapensis new species
Figs. 67–72, Map 4

Holotype.—Male from Caroline Islands, Yap, Fanif, shaken from dead lower banana leaves, 16 April 1980 (J.A. Beatty & J.W. Berry) (BPBM).

Etymology.—The species is named after the Yap group of islands in which it occurs.

Diagnosis.—The absence of a ventral fringe of setae from tibia I, the ventral spines of tibia I in two rows of 3–6 spines each, and the entirely granulate eye region (nowhere punctate or rugulose) distinguishes *S. yapensis* from all other species of the genus except *S. alboclypea* and *S. coriacea*. Absence of a band of white hairs on the clypeus (in both
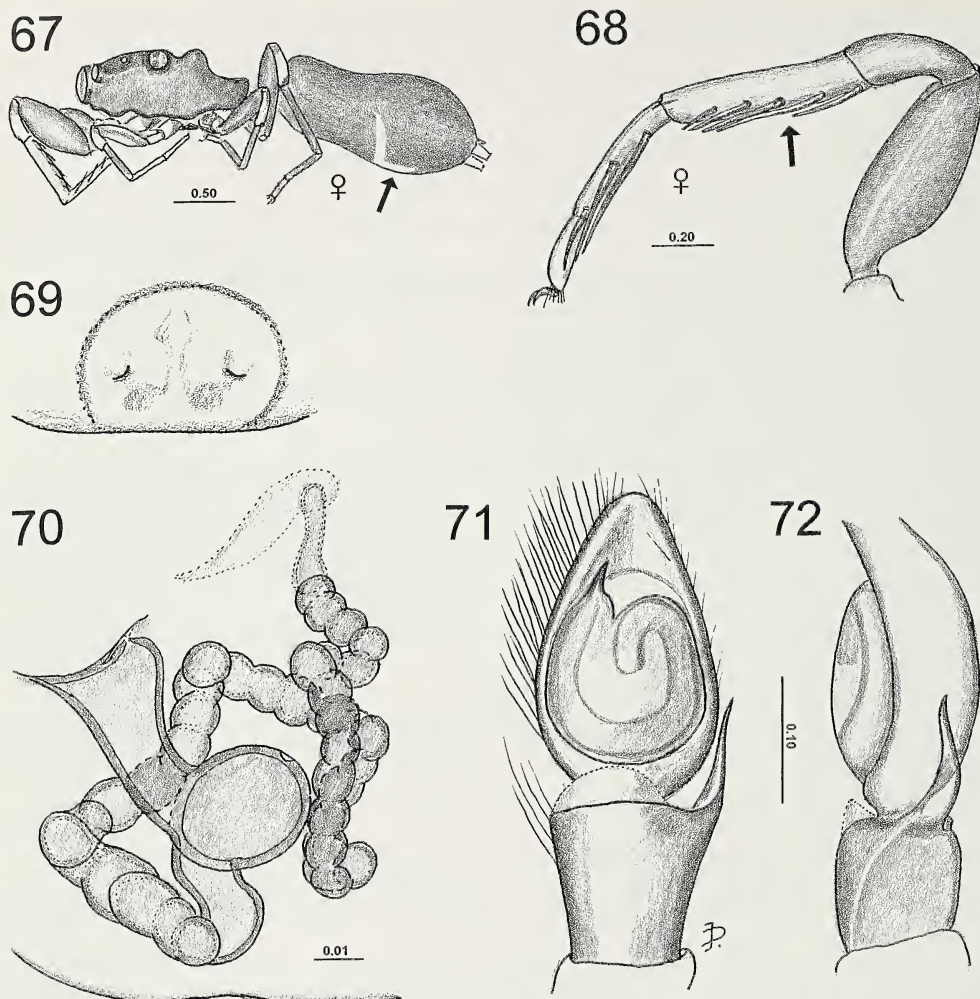
Figures 67–72.—*Sobasina yapensis* new species from Yap, Caroline Islands. 67, General appearance of female, with arrow indicating white diagonal line on abdomen; 68, Leg I of female, with arrow indicating tibial spines; 69, Diagram of epigynum (too small to observe details); 70, Internal structure of epigynum, showing right spermatheca and duct; 71, Palp of holotype male, ventrally; 72, Palp of holotype, laterally.

sexes) distinguishes it from *S. alboclypea* (known only from males). Quite similar to *S. coriacea,* from which it differs by having a retrolateral dark stripe on patella and tibia I, having a single transverse white abdominal band at the constriction of the abdomen, this band incomplete at the middle in females, and having the male abdominal scutum somewhat indistinct and partially divided at the constriction of the abdomen. Genitalic differences are more clearly indicated by the illustrations (Figs. 70–72, 76–79) than verbally.

Description.—*Male: (n = 5).* Total length 2.1–2.3 ($\bar{x}$ = 2.22), length of carapace 1.0–

1.1 ($\bar{x}$ = 1.03), maximum carapace width 0.65–0.68 ($\bar{x}$ = 0.67), eye field length 0.6–0.7 ($\bar{x}$ = 0.63), eye row I width 0.6–0.7 ($\bar{x}$ = 0.64). Cephalothoracic region without constriction behind eyes, or with only trace of it; chestnut brown with black pigment around lateral eyes and a small brown area between PME and PLE. Abdomen brownish dorsally, well sclerotized and shiny, with indistinct constriction in anterior half of abdomen, marked by a thin, white transverse line across dorsal and lateral surfaces of abdomen, interrupted dorsally and continuing along sides about halfway to end of abdomen. Face brown, ped-

ipalps light brown. *Legs:* Legs I, femur brown; tibia, patella and metatarsus yellow, thin, with darker, brown line along ventro-retrolateral edge, tibia I with (4 to 5)–(3 to 4) long ventral spines, of which the two median pairs are longer, metatarsus with three pairs of long spines. Remaining legs yellow, with femora III and IV brown. Leg formula 1–4–3–2, patella-tibia III<IV. Patella-tibia I length 0.6–0.8 ($\bar{x}$ = 0.72). *Palp:* Palpal tibia with single apophysis, relatively long bulb with anterior shoulder (Figs. 71, 72).

Female: (n = 5). Total length 2.9–3.2 ($\bar{x}$ = 3.05), length of carapace 1.2–1.3 ($\bar{x}$ = 1.25), maximum carapace width 0.7–0.8 ($\bar{x}$ = 0.77), eye field length 0.7–0.8 ($\bar{x}$ = 0.76), eye row I width 0.73–0.75 ($\bar{x}$ = 0.74). Cephalothoracic region with surface covered with small round warts, shiny, especially on eye field; chestnut brown with lateral eyes surrounded by black pigment, and a small brown area between PME and PLE. In comparison with *S. platypoda* new species broader, shorter, higher, PLE more protruding, depression behind eye field (Fig. 67) deeper but shorter, all thoracic region uniformly colored chestnut brown. Face brown, pedipalps light brown. Differs from *S. platypoda* new species in having tibia I long and narrow, without sclerotized edges. Abdomen dark grey, with indistinct constriction in anterior half of abdomen, marked also with a white diagonal line across lower sides. Mouth parts, sternum and coxae IV light brown, remaining coxae dark yellow, trochanters II-IV whitish; abdomen ventrally dark grey except short white line at the mid-length of marginal edge (Fig. 67). *Legs:* Legs I as in male, except tibial spines (5 to 6)–(4 to 5) (Fig. 68). Remaining legs with femora (especially III and IV) brown, whitish patellae, coxae and tarsi; tibiae and metatarsi darker yellow. Leg formula 1–4–3–2, with patella-tibia III<IV. Patella-tibia I length 0.8–0.9 ($\bar{x}$ = 0.84). *Epigynum:* Too small and indistinct to be clearly drawn, its structure shown in Figs. 69, 70. Spermatheca and its posterior duct-like part longer than in *S. coriacea,* moniliform for most of its length.

Material examined.—CAROLINE ISLANDS: *Yap,* Fanif, shaking dead banana leaves, 1♂1♀, 16 April 1980 (JAB & JWB). Fanif, tree shaking, 2♀, 16 April 1980 (JAB & JWB). Wanyan, dead coconut fronds, 2♂1♀ 1imm, 17 April 1980 (JAB & JWB). Wanyan, tree shaking, 1♀ 2imm, 16 April

1980 (JAB & JWB). Gilman, beach litter, 2♂1♀, 15 April 1980 (JAB & JWB). Gilman Point, beach litter, 2♂1♀, 29 May 1980 (JAB & JWB). Gilman Point, coconut undergrowth, 2♀, 29 May 1980 (JAB & JWB).

Distribution.—Known only from Yap in the Caroline Islands.

Sobasina platypoda new species
### Figs. 73–79, Map 4

Holotype.—Male from Fiji, Viti Levu, 22.4 km W of Suva, forest sweeping and shaking, 5 May 1987 (J.W. Berry & E.R. Berry) (BPBM).

Etymology.—The name *platypoda,* flat-footed, is based on the flattened dorsum of tibia I in both sexes (Fig. 75).

Discussion.—In contrast to other species which have considerable sexual dimorphism, both sexes in this species are quite similar (with exception of the leg length order; in males the first legs are longer, in females the fourth). The white line inside the abdominal constriction varies in width, and may be interrupted dorsally, but is present in both sexes. External appearance and tibia I very similar to *Efate raptor* (Berry et al. 1996) with which *S. platypoda* could at first be confused.

Diagnosis.—Distinguished from all other species of the genus by the fringe of flattened setae ventrally on tibia I and the short, deep tibia I with flattened dorsal surface and angular junction of its dorsal and lateral surfaces (Fig. 75). Not close to any other species of the genus in structure of first leg. Spermatheca and duct long, not moniliform (Fig. 79). Male palp (Figs. 76, 77) virtually indistinguishable from that of most other known males of the genus (see Fig. 92 and Wanless (1978) figs. 4A, 4I, 6E, 8D, and 8E).

Description.—*Male:* (n = 5). Total length 2.6–3.1 ($\bar{x}$ = 2.99), length of carapace 1.1–1.4 ($\bar{x}$ = 1.33), maximum carapace width 0.5–0.7 ($\bar{x}$ = 0.67), eye field length 0.5–0.7 ($\bar{x}$ = 0.69), eye row I width 0.5–0.7 ($\bar{x}$ = 0.63). Cephalothoracic region long and low, with surface shiny, especially on eye field covered with small round warts; chestnut brown with lateral eyes surrounded by black, a small brown area between PME and PLE; a patch of white adpressed setae on sides of cephalothorax above coxa II. Abdomen anteriorly light grey, posteriorly darker, divided by a distinct constriction and a broad white ring or a
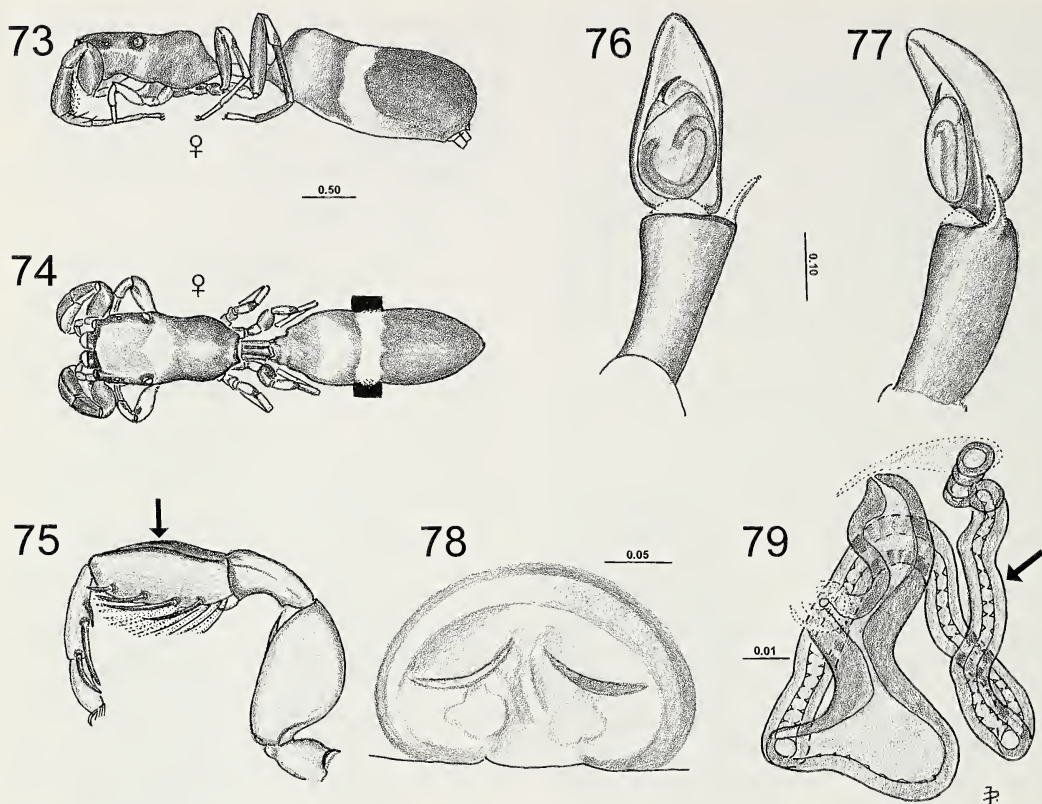
Figures 73–79.—*Sobasina platypoda* new species from Viti Levu, Fiji. 73, Lateral view of female; 74, Dorsal view of female (black marker to emphasize white abdominal banding); 75, Leg I, showing fringe on tibia and angular junction of dorsal and lateral surfaces; 76, Palp of holotype male, ventrally; 77, Palp of holotype male, laterally; 78, Epigynum; 79, Internal structure of epigynum, showing chamber of right spermatheca and thicker-walled duct-like posterior extension of spermatheca.

thin line. Pedipalps light brown. *Legs*: Tibia I distinctly broad and short, with sclerotized edge. Legs I brown except two terminal segments which are whitish-yellow, differing from *Sobasina yapensis* new species in having tibia I shorter but twice broader dorsally, with sclerotized edges, somewhat swollen ventrally, with dense row of long dark setae along ventral surface, between two rows of 4 to 5 ventral spines. Leg II entirely whitish, legs III and IV with femora and tibiae brown, metatarsi dark yellow, tarsi and patellae whitish, the latter with apical darker spot. Sternum and coxae of legs III-IV chestnut brown, remaining coxae dark yellow to brown, trochanters I-III brown, but white on IV. Leg formula 1≈4–3–2, patella-tibia III<IV. Patella-tibia I length 0.5–1.0 ($\bar{x}$ = 0.89). *Palp:* Proportions of pedipalps differ from other species in having tibia longer and thinner; embolus short and curved, located slightly more posteriorly,

slightly protruding in front of apex of the bulb and parallel to it; tibial apophysis smaller and thinner, sometimes transparent (Figs. 76, 77).

Female: (n = 5). Total length 3.3–3.8 ($\bar{x}$ = 3.58), length of carapace 1.3–1.5 ($\bar{x}$ = 1.41), maximum carapace width 0.7–0.8 ($\bar{x}$ = 0.71), eye field length 0.6–0.8 ($\bar{x}$ = 0.72), eye row I width 0.6–0.7 ($\bar{x}$ = 0.67). Sexes are remarkably similar to each other, an exception in this genus. Cephalothorax narrower, longer, lower than in females of *Sobasina yapensis* new species, PLE less protruding, depression behind eye field shallower but longer, lighter colored, from it a slightly lighter streak runs to the thoracic rear margin. *Legs:* Leg formula 4–1–3–2, patella-tibia III<IV. Patella-tibia I length 0.7–1.0 ($\bar{x}$ = 0.87). *Epigynum:* So small that the drawing (Fig. 78) gives only its approximate shape; internal structure differs by constriction of spermatheca into two chambers

and shape of the thicker walled duct-like posterior extension of spermatheca (Fig. 79).

Material examined.—**FIJI**: *Viti Levu,* Suva, Queen Elizabeth Drive, on mangrove leaf, 1♀, 9 May 1987 (JAB). Forest sweeping & shaking, 22.4 km W of Suva city, 1♂, 5 May 1980 (JWB & ERB). Lami, 0–350 m, 2♂, March 1978 (N.L.H. Krauss). SW of Lami, 9 km W of Suva, cut-over forest, 1♀ 1imm, 23 May 1987 (JWB & ERB). About 5 miles W of Nausori, Nanduruloulou Research Station, 1♀, 15 May 1980 (JAB). Nausori Highlands Forest Reserve, Leveitoko Block, elev. 1500 ft., shaking/picking, 2♂1♀, 27 May 1987 (JWB & ERB). Nausori, Koronivia Research Station, sweeping & shaking trees, 1♂1♀, 8 May 1987 (ERB). Nandarivatu, 1100 m., 1♀ 1imm, 23 December 1963 (J.L. Gressitt) (BPBM). Nandarivatu, 1♀ 1imm, 1 November 1938 (E.C. Zimmerman) (BPBM). Nandarivatu, 2700 ft, 1♂, 18 July 1938 (E.C. Zimmerman) (BPBM). Nandarivatu, on shrub, elev. 900 m, 1♂1♀, 11 April 1987 (JAB). Nandala creek, 2 mi. S of Nandarivatu, sweeping & shaking, 3♂2♀ 2imm, 12 April 1987 (ERB). Nandarivatu, pine/shrub forest beside guesthouse, sweeping & shaking, elev. 800 m., 1♀ 1imm, 14 May 1987 (JWB & ERB). Nandarivatu, 2700 ft., 1♂, 18 July 1938 (BPBM). Nandarivatu, 1♀, 1 September 1938 (E.C. Zimmerman) (BPBM). Tholo-I-Suva Forest Park, Waisila Falls Trail, sweeping, 1♂ 1imm, 11 May 1987 (JWB). Tholo-I-Suva, 1♀ 1imm, 27 July 1938 (BPBM). 7 mi. N of Singatoka, sweeping/shaking shrubs along river, 1♂, 21 May 1987 (JWB & ERB). Hill forest about 8 miles NE of Navua, tree shaking, 1♂, 2 May 1987 (JWB & ERB). Belt Road, 2♀, 22 July 1938 (BPBM). Lami, 0–350 m, 1♂, March 1978, (N.L.H. Krauss) (BPBM). *Ovalau,* Levuka, 1♀, December 1969 (N.L.H. Krauss) (BPBM). Wai-ni-loka, 1♀, 11 July 1938 (Z-45) (BPBM). Levuka, 1♀, December 1969 (Krauss) (BPBM).

Distribution.—Known only from Viti Levu and Ovalau islands of Fiji.

Sobasina coriacea new species
Figs. 80–85, Map 4

Holotype.—Holotype female from Palau: Koror Island, Entomology Lab., banana trash below lab (in ravine), 9 March 1973 (J.W. Berry & J.A. Beatty).

Etymology.—The species name *coriacea,* leathery, is given because of the presence of a dorsal abdominal scutum in the male.

Diagnosis.—The lack of ventral setal fringe on tibia I, ventral spination of tibia I (5-(4 to 5)) and eye region uniformly granulate distinguish *S. coriacea* from all other species of the genus except *S. alboclypea* and *S. yapensis.* From *S. alboclypea* (known only from males) it is separated by the absence (in both sexes) of a band of white setae on the clypeus. The female differs from that of *S. yapensis* by having two transverse white bands on the abdomen, one across the abdominal constriction and another more anterior (Fig. 81) (single incomplete band at the constriction in *S. yapensis*), by the absence of a dark prolateral stripe on tibia and patella I and by the shorter epigynal duct plus spermatheca, which is moniliform for about half its length (Fig. 85). The male of *S. coriacea* has a distinct undivided abdominal scutum, unconstricted abdomen (Fig. 80), and no dark prolateral stripe on tibia and patella I. (Scutum somewhat indistinct and divided, abdomen constricted aand dark stripe present on tibia and patella I in *S. yapensis.*)

Description.—*Male:* ($n = 5$). Total length 2.0–2.3 ($\bar{x} = 2.07$), length of carapace 1.0–1.1 ($\bar{x} = 1.01$), maximum carapace width 0.6–0.7 ($\bar{x} = 0.67$), eye field length 0.5–0.7 ($\bar{x} = 0.60$), eye row I width 0.6–0.7 ($\bar{x} = 0.67$). Cephalothorax sloping abruptly behind eye field, its dorsal surface slightly rounded; no dorsal depression like that in female, but pigmentation difference makes some appearance of it. Surface of eye field covered with minute warts. Cephalothorax light chestnut brown, with black around lateral and anterior eyes, eye field darker; irregular grey lines radiating from front to edge of the thoracic region. Abdomen covered with shiny scutum, brown, without constriction or white transverse line. Sides with a dark grey linear pattern, separated by chains of small, lighter dots. *Legs:* Legs II-IV brownish-yellow, femora IV with darker lateral streak along apical half; Legs I with femur and basal part of metatarsus dark brown, tibia long, thin with two rows of ventral spines of 4 to 6 spines each, the 2nd and 3rd being very long, metatarsus I with three pairs of long ventral spines. Leg formula 1–4–2–3, patella-tibia III<IV. Patella-tibia I length 0.6–0.8 ($\bar{x} = 0.71$). *Palp:* Bulb of palp (Figs. 83, 84) lacking the projecting shoulder, lateral to the embolus, found in most other species.

Female: ($n = 5$). Total length 2.3–3.0 ($\bar{x} = 2.67$), length of carapace 1.1–1.3 ($\bar{x} = 1.21$), maximum carapace width 0.7–0.8 ($\bar{x} = 0.74$), eye field length 0.7–0.8 ($\bar{x} = 0.73$), eye row
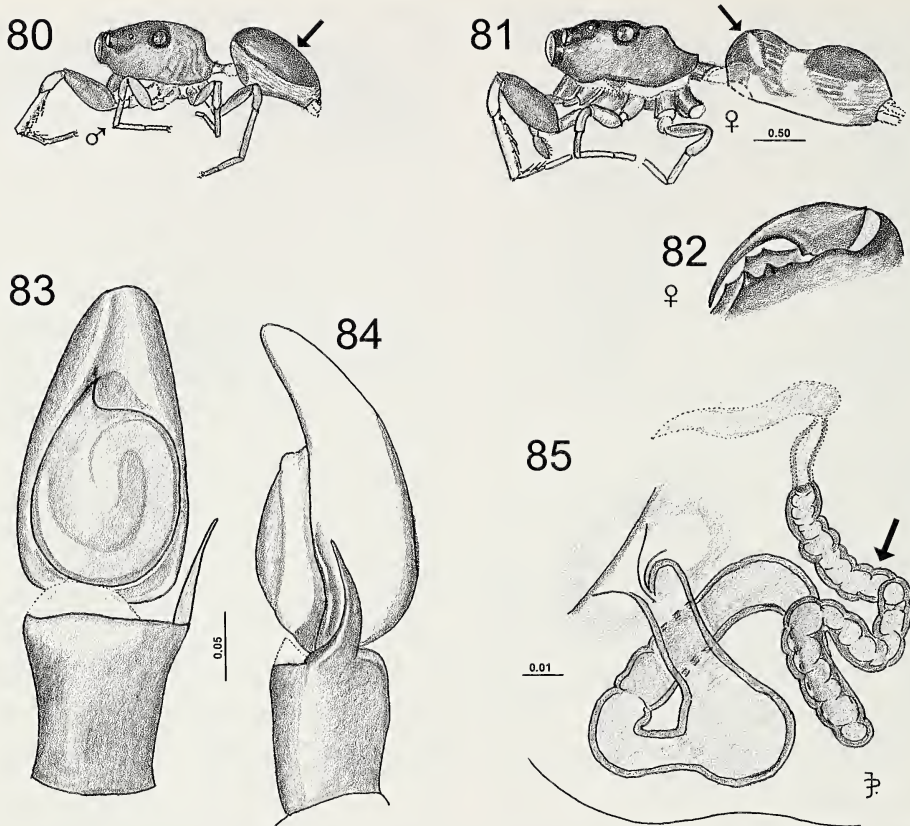
Figures 80–85.—*Sobasina coriacea* new species from Palau, Caroline Islands. 80, Lateral view of male, with arrow indicating undivided abdominal scute and unconstricted abdomen; 81, Lateral view of holotype female, with arrow indicating anterior abdominal white band; 82, Cheliceral dentition of holotype female; 83, Palp ventrally; 84, Palp laterally; 85, Internal structure of epigynum of holotype, showing right spermatheca and duct, with arrow indicating the moniliform nature of duct (epigynum itself too indistinct to illustrate).

I width 0.7–0.8 (x̄ = 0.75). Resembles females of S. *amoenula* and *yapensis*. *Legs:* Leg formula 4–1–3–2, patella-tibia III<IV. Patella-tibia I length 0.7–1.0 (x̄ = 0.87). *Epigynum:* Internal structure resembles that in *Sobasina yapensis* new species, from which *coriacea* differs by the shorter posterior, duct-like part of the spermatheca which is moniliform for only half its length or less (Fig. 85). An indistinct swelling of the entrance duct just behind the copulatory opening comparable to that in S. *yapensis* new species.

Material examined.—CAROLINE ISLANDS: *Palau,* Koror, taro patch litter, 1♂2♀, 26 March 1973 (JWB & JAB). Koror, taro patch litter, 1♂, 30 March 1973 (JAB & JWB). Koror, banana trash below lab (in ravine), 1♀ (holotype), 9 March 1973 (JAB & JWB). Koror, scrub forest in vacant lot, grass litter, 1♂, 13 February 1973 (JWB). Koror,

vacant lot, grass litter, 1♂ 1imm., 15 February 1973 (JWB). Koror, vacant lot, litter, 1♀, 13 March 1973 (JWB & JAB). Koror, compost pile, 1♂, 30 March 1973 (JWB & JAB). Koror, taro patch #2, litter, 1♂ 1imm, 3 April 1973 (JAB & JWB). Arakabesan, mixed tropical forest litter, elev. 20 ft., 1♂, 28 February 1973 (JWB). Babelthuap, Airai, betel palm fronds, 1♀, 11 March 1973 (JAB & JWB). Babelthuap, Airai, tropical forest, 1♀, 27 March 1973 (JAB & JWB). Peleliu, rock island forest litter, 1♂2♀ 2imm, 22 March 1973 (JWB & ERB).

Distribution.—Known only from the Palau group of the Caroline Islands.

Sobasina cutleri new species
Figs. 86–89, Map 4

Holotype.—Male from Fiji, Viti Levu, Nandarivatu, 870 m, 9 January 1987 (N.I. Platnick) (AMNH).
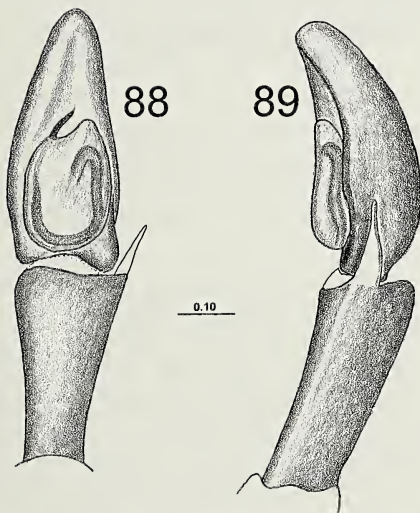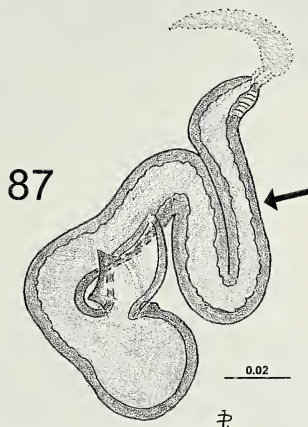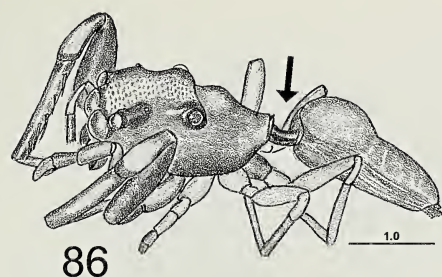
Figures 86–89.—*Sobasina cutleri* new species from Viti Levu, Fiji. 86, General appearance of male holotype, with arrow indicating long pedicel; 87, Internal structure of epigynum showing right spermatheca and non-moniliform duct; 88, Palp of holotype, ventrally; 89, Palp of holotype, laterally.

Etymology.—This species is named for Dr. Bruce Cutler of the University of Kansas in Lawrence, Kansas, in recognition of his work in the family Salticidae.

Diagnosis.—No fringe of flattened setae on tibia I, ventral spines of tibia I in two rows of 5 to 6 spines each, eye region and sides of thoracic region with conspicuous punctures, pedicel long (Fig. 86). No other species of the genus fits this description. Internal structure of epigynum (Fig. 87) without moniliform spermatheca. Embolus, anterior shoulder of bulb and tibial apophysis (Figs. 88, 89) somewhat longer than in other species except for *S. solomonensis* and *S. platypoda,* which are distinguished by non-genitalic characters cited above.

Description.—*Male:* ($n = 2$). Total length 3.9, 4.0, length of carapace 1.9, 2.1, maximum carapace width 1.0, 1.2, eye field length 1.1, 1.2, eye row I width 0.9, 1.1. Cephalothorax dark brown, punctate all over, except top of the thoracic protuberance, PLE on protuberances, much higher above the dorsum and sides of cephalothorax than in other species. Petiole with long anterior sclerite, posterior sclerite not visible. Abdomen elongate, in male without constriction, the anterior part forming an indistinct, rounded bulge; light greyish-brown, with weak traces of lighter diagonal lines in the posterior half. Pedipalps chestnut brown, with patella lighter, narrow and slender. In ventral aspect, mouth parts, sternum and coxa IV brown, remaining coxae and trochanters yellow, abdomen anteriorly brownish-grey, behind epigastric fold pale yellow, framed with dark grey, yellow punctate sides, spinnerets grey. *Legs:* Leg I brown and longer than others, femur I with trochanter and coxa elongated, femur I broader and darker than remaining segments, tibia I cylindrical with five pairs of ventral spines; remaining legs slender and yellow, tibia II with 1–0 retroventral ventral spines. Leg formula 1–4–3–2, patella-tibia III<IV. Patella-tibia I length 1.5, 1.8. *Palp:* (Figs. 88, 89). Palp with embolus longer than in other species, anterolateral projection of bulb reaching near end of embolus, tibial apophysis long. In these features resembling *S. solomonensis* and *S. platypoda,* from which it differs by non-genitalic characters.

Female: ($n = 5$). Total length 3.1–5.0 ($\bar{x} = 4.27$), length of carapace 1.4–2.3 ($\bar{x} = 1.97$), maximum carapace width 0.5–1.1 ($\bar{x} = 0.98$), eye field length 0.9–1.3 ($\bar{x} = 1.17$), eye row I width 0.5–1.1 ($\bar{x} = 0.93$). Sexes very similar. Abdomen with traces of constriction and of
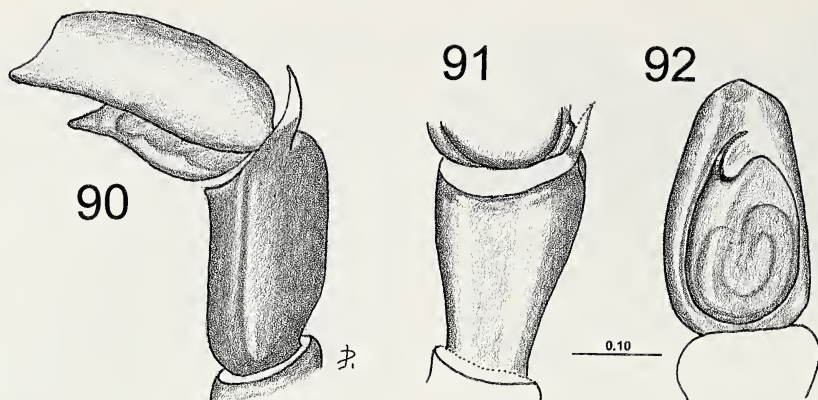
Figures 90–92.—*Sobasina aspinosa* new species from Vanua Levu, Fiji, holotype male. 90, Palp laterally; 91, Palpal tibia ventrally; 92, Cymbium and bulb ventrally.

dark coloration, on sides horizontal dark grey lines separated by thinner light ones. Pedipalps as brown as femur I, much darker than tibia I dorsally. *Legs:* Patella-tibia I length 0.9–1.7 ($\bar{x}$ = 1.21). Legs comparable with male, but legs II-IV appear darker. Leg formula 4–1–3–2, patella-tibia III<IV. *Epigynum:* A membranous opening leading almost directly to spherical spermathecal chamber, from which branches a large triangular structure. Posterior part of spermatheca duct-like, doubly curved, but otherwise much simpler than in other species (Fig. 87).

Material examined.—FIJI: *Viti Levu,* Nandarivatu, 870 m., 1♂ (holotype), 9 January 1987 (N.I. Platnick) (AMNH). Nandarivatu, Loma Lagi trail, in litter, 1♂, 15 April 1987 (JAB). Nandarivatu, 1100 m, 1♀ 1imm, 23 December 1963 (J.L. Gressit) (BPBM). Nandarivatu, 1♀ 1imm, 1 September 1938 (E.C. Zimmerman) (BPBM). Nandarivatu, 2♀ 3imm, 10 September 1938 (E.C. Zimmerman) (BPBM). Nausori highlands, 500–700 m, 3♀, November 1976 (N.L.H. Krauss). *Ovalau,* Wai-niloka, 1♀, 11 July 1938 (Z-47) (BPBM).

Distribution.—Known only from Viti Levu and Ovalau Islands, Fiji.

Sobasina aspinosa new species
Figs. 90–92, Map 4

Holotype.—Male from Fiji, Vanua Levu, Malaise trap, G.A. Samuelson, 1979 (BPBM).

Etymology.—The name *aspinosa,* spineless, refers to the absence of spines from the legs of this species.

Diagnosis.—Tibia I very thin and long, legs without any spines, pedicel very long; eye field finely rugose, punctures along sides

of thoracic region, single row of distinctly larger punctures along ventral edge of cephalothorax.

Description.—*Male:* (n = 2). Total length 3.9, 4.0; length of carapace 1.9, 2.0; maximum carapace width 0.9, 1.0; eye field length 0.9, 1.0; eye row I width 0.9, 0.9. Eye field dark brown, very finely rugose, same as sides below anterior eyes; rows of minute punctures along lower sides of thoracic region, a single row of distinctly larger punctures along ventral edge of cephalothorax; a few minute white setae on cephalothorax are slightly broadened. A patch of white adpressed setae located above base of coxa I. Abdomen covered by uniform dark, hard, shiny scutum, with distinct traces of constriction and a lateral patch of white setae. Frontal aspect dark brown, chelicerae broad and robust. *Legs:* Legs totally without spines, very thin; the retrolateral surface of femur I and both lateral surfaces of remaining segments of leg I darker, their ventral and dorsal surfaces much lighter. Leg formula 1–4–3–2, patella-tibia III<IV. Patella-tibia I length 1.2, 1.3. *Palp:* Broader, more robust than in remaining species (Figs. 90–92).

Female: The female is unknown.

Material examined.—FIJI: *Viti Levu,* Namosi road, 7.7 km N of Queen's Road, roadside sweeping & shaking, 1♂, 7 May 1987 (JWB, ERB & JAB). *Vanua Levu,* Malaise trap, 1♂ (holotype), G.A.S., 1979, 221 (BPBM).

Distribution.—The islands of Viti Levu and Vanua Levu, Fiji.
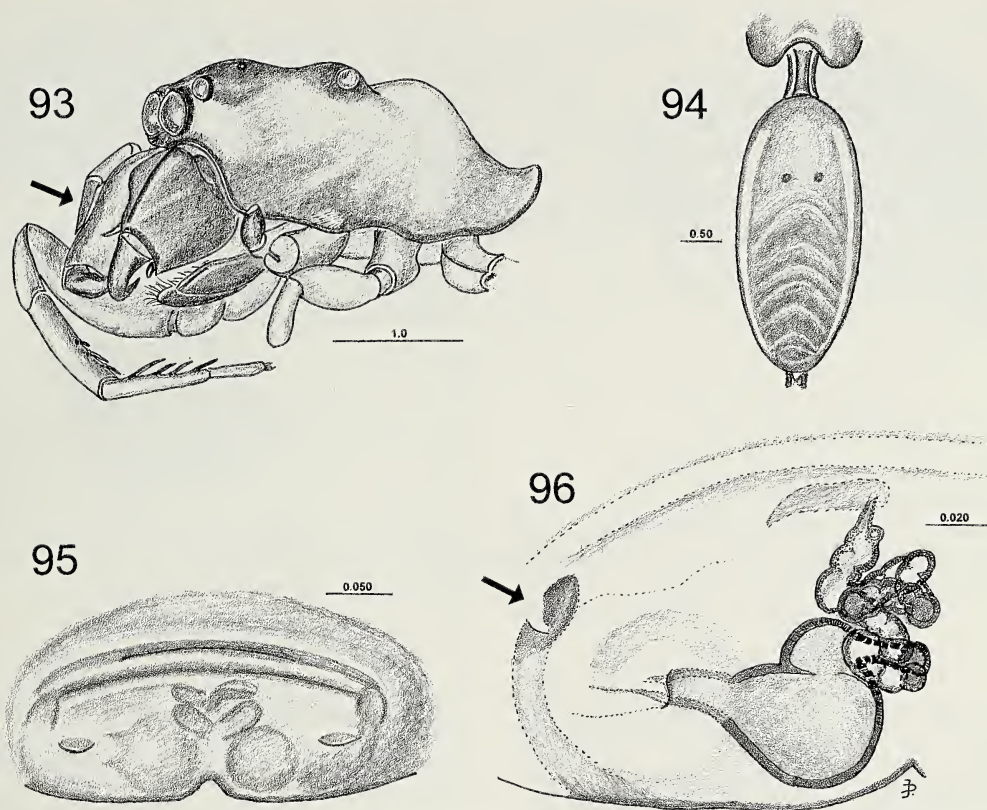
Figures 93–96.—*Sobasina magna* new species from Eua, Tonga, holotype female. 93, Lateral view of female cephalothorax, with arrow indicating swollen, triangular chelicerae with prominent sclerotized external angles; 94, Abdominal pattern of female; 95, Epigynum; 96, Internal structure of epigynum showing right spermatheca and duct, with arrow showing dark oval structures without visible connection to internal structures.
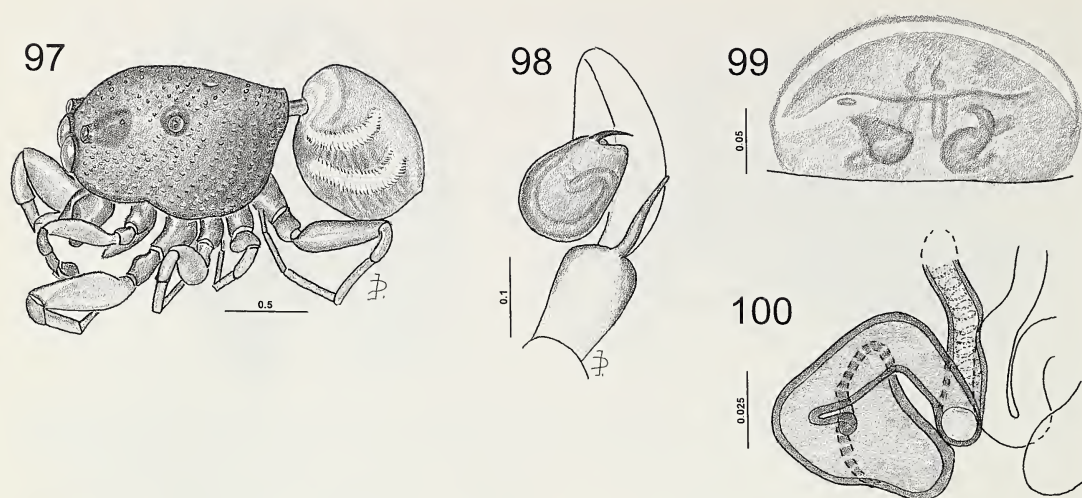
Sobasina magna new species
Figs. 93–96, Map 4

Holotype.—Female from Tonga, Eua, 0–100 m, 1979 (N.L.H. Krauss) (BPBM).

Etymology.—The name *magna,* large, is in reference to the fact that this is the largest species of *Sobasina* thus far known.

Diagnosis.—Large (7.1 mm) and broad, cephalothorax constricted, but the abdomen not; chelicerae large, swollen and diverging, with prominent, sclerotized angles and a huge promarginal tooth, retromargin with one large apical and a small bicusp basal tooth. Tibia I cylindrical and long, with spines smaller than in other species and located ventrally in the apical half, two retrolateral and three prolateral. Epigynum very small, its internal structure as in Figs. 95, 96.

Description.—*Female:* (*n* = 1). Total length 7.1, length of carapace 3.0, maximum carapace width 1.8, eye field length 1.5, eye row I width 1.4. Cephalothorax anteriorly dark brown with black around lateral and anterior eyes, posteriorly lighter, fawn, with thoracic swelling almost yellow. Anterior part of eye field covered with semicircular papillae, each bearing a minute whitish seta; posteriorly surface is rough but without regular papillae, thoracic swelling smooth. A distinct dorsal thoracic swelling behind eye field, separated by shallow lateral grooves, but no dorsal groove (Fig. 93). Lower sides dark brown, with a small, triangular patch of adpressed white setae above coxa I. *Chelicerae*: Large, swollen, triangular, diverging, dark brown, with external angles prominent and sclerotized. One bicusp retromarginal cheliceral tooth, and an additional rounded tooth at base of fang, two promarginal cheliceral teeth, one greatly enlarged. Face dark, with eyes sur-

Figures 97–100.—*Sobasina paradoxa* new species from Viti Levu, Fiji. 97, General appearance of male; 98, Ventral-lateral view of palp (somewhat foreshortened) with bulb expanded; 99, Epigynum; 100, Internal structure of epigynum, ventral view. (Drawn from specimens from Mt. Tomanivi.)

rounded by sparse inconspicuous setae, clypeus very low, no contrasting marks. Pedipalp yellow, with tibia brown, tarsus missing. Mouth parts dark brown, sternum brown with darker margins. Abdomen not ant-like in character; elongate, oval, narrowing posteriorly, greyish-fawn with white marginal streaks and indistinct lighter dorsal chevrons (Fig. 94). Abdomen greyish ventrally. *Legs:* Legs relatively slender, almost without spines. Coxae I–III yellow, coxae IV brown; yellow except femur I brown, and darkened lateral surfaces of patella, tibia and metatarsus I. Tibia I peculiar by limitation of spines to its apical half; tibia cylindrical, thin and long; spines relatively smaller than in other species. Metatarsus I with three pairs of ventral spines, evenly distributed. Leg formula 1–4–2–3, patella-tibia III<IV. Patella-tibia I length 2.2. *Epigynum:* Very small, transversely oval, with indistinct transverse anterior groove (Fig. 95); two darker oval structures laterally, with small openings but without visible connection with internal structures. Openings lateral, very indistinct, apparently membranous, short, soft-walled duct leads to spherical spermathecae, extended by a narrow duct, making a series of complicated loops, forming a tightly entangled knot medially and anteriorly to spherical chamber.

Male: The male is unknown.

Material examined.—Only the holotype.

Distribution.—Known only from the type locality in Tonga.

Sobasina paradoxa new species
Figs. 97–100, Map 4

Holotype.—Male from Fiji, Viti Levu, Nandarivatu, 3700 ft., 9 October 1938 (E.C. Zimmerman) (BPBM).

Etymology.—The name *paradoxa* is based on the unusual body form of the species, as compared with other members of the genus.

Discussion.—This species is so different in body form from all other species of the genus that its placement in *Sobasina* may be questioned, but if the genitalia are considered of prime importance in defining salticid genera, regardless of somatic differences, then *Sobasina* is the proper genus. The simplicity of the genitalia may make reliance on them unwise, however. Rather similar male palps occur in the genera *Hasarius, Heratemis, Rogmocrypta, Simaetha* and probably others. Given our state of knowledge of salticids in general we conclude that relying first on the genitalia is the best course for the present.

Diagnosis.—Somewhat beetle-like, resembling *Coccorchestes* by very strongly sclerotized tegument of cephalothorax, with rows of circular punctures which cover the entire car-

apace (Fig. 97); differs by absence of crenel-
lated shelf at posterior cephalothorax, with
posterior edge coming below anterior abdo-
men. Entire carapace punctured. Pedicel hid-
den beneath abdomen. Constrictions absent
from both cephalothorax and abdomen. Tibia
I without fringe of setae.

Description.—*Male: (n = 5).* Total length
2.2–2.4 ($\bar{x}$ = 2.3), length of carapace 1.3–1.4
($\bar{x}$ = 1.36), maximum carapace width 0.95–
1.0 ($\bar{x}$ = 0.97), eye field length 0.65–0.80 ($\bar{x}$
= 0.75), eye row I width 0.75–0.85 ($\bar{x}$ =
0.81). Cephalothorax with prominent, steep
anterior slope of the eye field between ALE;
ALE are located distinctly above AME. Dor-
sum levels at about the second eye row and
continues flat from there back, narrowing pos-
teriorly but without any dorsal constriction or
depression; tegument of cephalothorax strong-
ly sclerotized, with rows of circular pits. Ped-
icel arises from cephalothorax very dorsally.
Abdomen oval, broad, slightly flattened, with-
out any traces of constriction, either dorsal or
lateral. Two diagonal rows of whitish scales
along anterior part of sides of abdomen. *Legs:*
Leg formula 1–4–2–3; patella-tibia III<IV.
Spination, tibia I 3–3 ventral; metatarsus I 3–
3, tibia II ventral, none; metatarsus II ventral
1–0. No other leg spines. *Palp:* Bulb and em-
bolus as in *S. platypoda* and *S. aspinosa*; tibial
apophysis longer than in those species (Fig.
98).

Female: (n = 3). Total length 2.1–3.0 ($\bar{x}$ =
2.7), length of carapace 1.2–1.6 ($\bar{x}$ = 1.5),
maximum carapace width 0.9–1.2 ($\bar{x}$ = 1.06),
eye field length 0.7–1.0 ($\bar{x}$ = 0.86), eye row
I width 0.7–0.9 ($\bar{x}$ = 0.86). Cephalothorax as
in male except for ALE located slightly above
AME. Abdomen as in male. *Legs:* Leg for-
mula 4–1–2≈3; patella-tibia III<IV. Spina-
tion, tibia I 4–4 ventral; metatarsus I 3–3, tib-
ia II ventral 1–0; metatarsus II ventral 2–0.
No other leg spines. *Epigynum:* With trans-
verse rim near middle of length; connecting
ducts short and not highly convoluted, similar
to *S. cutleri* (Figs. 99, 100).

Material examined.—Fiji, Viti Levu, Nandari-
vatu, 3700 ft., 6♂ (including holotype) 2♀ 3imm,
9 October 1938 (E.C. Zimmerman) (BPBM); Mt.
Tomanivi (= Mt. Victoria), 1320 m., summit moss
forest, moss litter, 4♂3♀ 5imm, 20 August 1978
(S. & J. Peck) (AMNH).

Map 5.—Distribution of five species of the new
genus *Xenocytaea* in the Pacific. *Xenocytaea tri-
ramosa* new species (○), *Xenocytaea zabkai* new
species (●), *Xenocytaea daviesae* new species (□),
Xenocytaea maddisoni new species (■) and *Xeno-
cytaea anomala* new species (★).

Distribution.—Known only from Viti
Levu of the Fiji islands.

Genus *Xenocytaea* new genus
Figs. 101–121; Map 5

Type species.—*Xenocytaea triramosa* new
species, from Viti Levu, Fiji.

Etymology.—From Greek, *xeno,* strange or
foreign, and the generic name, *Cytaea,* to in-
dicate that, despite the similarity in male pal-
pal structure, this group of species does not
belong in *Cytaea.* The genus is feminine.

Discussion.—A survey of all 150 salticid
genera known from Australia and the entire
Pacific, exclusive of Japan and New Zealand,
found only three genera that resemble *Xeno-
cytaea*: *Chalcotropis, Donoessus* and *Panysi-
nus.* With the exception of *Hasarius insularis*
Keyserling 1881 from Tonga, now placed in
Chalcotropis, these genera are not known
from the area considered here. *Hasarius
mccooki* Thorell 1892 may belong in this ge-
nus.

Diagnosis.—The cheliceral dentition (bi-
cusp retromarginal tooth and two promarginal
teeth), presence of lateral spines on patellae,
tibiae and metatarsi, and ventral spination on
tibia I, 2–2 or fewer (except in *X. anomala*)
separate *Xenocytaea* from all other salticid
genera of the entire Pacific except possibly
Chalcotropis Simon 1902, *Donoessus* Simon
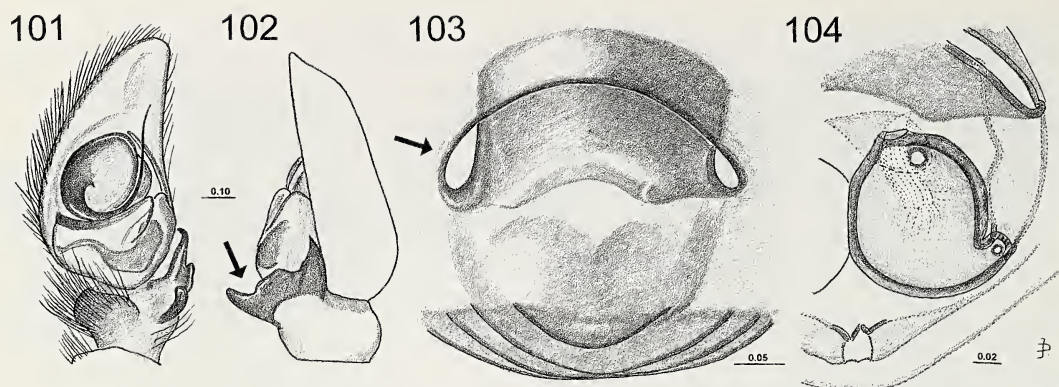
Figures 101–104.—*Xenocytaea triramosa* new species from Viti Levu, Fiji. 101, Palp of holotype male, ventrally; 102, Palp of holotype male, laterally, with arrow indicating tripartite tibial apophysis; 103, Epigynum, with arrow indicating opening at edge of arch; 104, Internal structure of epigynum, showing left spermatheca and ducts.

1902 and *Panysinus* Simon 1901. From these genera it is distinguished (except *X. anomala*) by the epigynal arches (Figs. 103, 106, 110, 114), and absence of a conductor-like process from the male palp (Figs. 102, 108, 112).

Description.—Small fissident salticids with the retromarginal cheliceral tooth usually narrow and bifurcate, with two promarginal teeth. Female chelicerae brown, slightly bulging basally, rounded. With a lateral spine on each side on patellae III and IV, and a prolateral one on I or I and II. With 2–2 ventral spines on tibia I (3–3 in *anomala*) and at least some lateral spines on most or all tibiae and metatarsi. A dorsal spine near the base on tibiae III and IV.

Male palp resembling that of *Cytaea,* with the embolus forming a flat coil on the ventral surface of the bulb, making one or two counterclockwise turns, the bulb wide and often projecting beyond the cymbium. Epigyna (except *anomala*) with widely separated openings located under the ends of an anterior arch (Figs. 103, 106, 110, 114), the ducts short and little coiled. In three species (*zabkai, daviesae* and *maddisoni*) a posterior pocket present, also (Figs. 106, 110, 114). Epigynum of *anomala* somewhat resembling that of *Ascyltus* and some species of *Cytaea* (see Figs. 10, 11, 14, 19, 23, 28, 34).

Cephalothorax usually unicolorous in the male, never with the U-shaped light and dark bands characteristic of many *Cytaea.* Abdominal color pattern of females lacking the broad median longitudinal band of *Cytaea.*

## *Xenocytaea triramosa* new species
Figs. 101–104; Map 5

Holotype.—Holotype male from Fiji, Viti Levu, Nausori Dist., hill forest on Namosi Road about 7 km N of Queen's Road, 19 May 1987 (J.W. & E.R. Berry) (BPBM).

Etymology.—The specific name, *triramosa,* refers to the three-part retrolateral tibial apophysis of the male palp.

Diagnosis.—Broad flattened pedipalpal femur and patella and three-part tibial apophysis in male, and epigynum with openings not covered by arch, spermatheca globular, distinguish this species from the others of the genus.

Description.—*Male:* ($n = 3$). Total length 3.9–4.5 ($\bar{x} = 4.25$), length of carapace 2.1–2.3 ($\bar{x} = 2.17$), maximum carapace width 1.5–1.7 ($\bar{x} = 1.58$), eye field length 1.1–1.2 ($\bar{x} = 1.17$), eye row I width 1.45–1.50 ($\bar{x} = 1.48$). Cephalothorax dark brown, eye field with white adpressed setae, a few orange setae around PLE; a few spots of white setae on sides of thoracic region. Frontal aspect light brown, with anterior eyes indistinctly surrounded with whitish setae, clypeus appearing bare. Chelicerae brown, the anterior surface depressed, making a triangular space along apical half of both chelicerae. Abdomen with marginal parts of dorsal surface greyish, median streak white, bisected anteromedially by darker line; two longer transverse white lines, the median connecting two small round spots, the posterior expanded diamond-shaped cen-
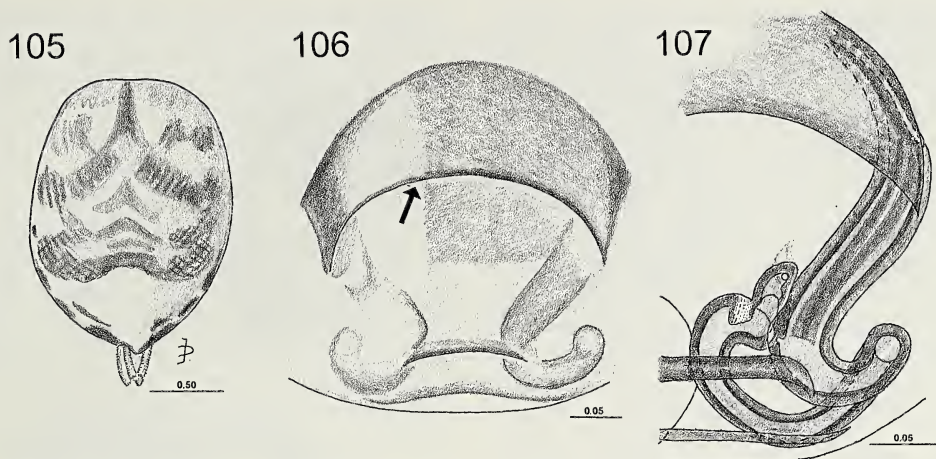
Figures 105–107.—*Xenocytaea zabkai* new species from Viti Levu, Fiji, holotype female. 105, Abdominal pattern; 106, Epigynum, with arrow indicating copulatory openings hidden under arch; 107, Internal structure of epigynum, showing left spermatheca and ducts.

trally, between them a shorter white line. Leg I and pedipalps contrastingly colored blackish-brown and whitish. Dorsal surface of pedipalpal femur broad, flattened, shiny dark brown, bordered retrolaterally by a row of stiff black setae, basally by much longer white setae. Patella, tibia and cymbium dorsally broad and flattened, prolaterally black with long, black setae, contrasting with white dorsal surface of cymbium and parts of tibia and patella. *Legs:* Legs I blackened on prolateral half of dorsal surfaces of tibia and metatarsus I, these are also ornate with black ventral crests of long setae and a retrolateral row of white setae. Legs III-IV greyish-yellow, with tibiae II-IV slightly darker dorsally, ventral surfaces of tibiae II-III black; femora I-IV whitish, except ventral surface of femur II blackened. Leg formula 3–4–1=2; patella-tibia III≅IV. Patella-tibia I length 1.4–1.5 ($\bar{x}$ = 1.47). *Palp:* Embolus makes flat coil on the ventral, anterior surface of bulb; tibial apophysis tripartite, the lateral portions triangular, middle section truncate (Figs. 101, 102).

Female: (n = 1). Total length 5.6; length of carapace 2.5;, maximum carapace width 1.8, eye field length 1.3; eye row I width 1.7. Cephalothorax almost uniformly dark brown, eye field covered with white adpressed setae, a few orange setae below PLE. A few long upright bristles behind PLE, similar on eye field, becoming gradually lower anteriorly. Abdomen covered with minute dark setae and a few patches of minute white scales, traces of grey pattern with lighter median streak along posterior half and two transverse white lines, the median longer and the posterior shorter. Frontal aspect light brown, with anterior eyes indistinctly surrounded with whitish setae, clypeus yellowish, almost entirely bare with three curved bristles. *Legs:* Leg I and pedipalps with femora whitish, remaining segments slightly darker, with sparse short dark setae. Leg formula 4–3–1–2, patella-tibia III≅IV. Patella-tibia I length 1.5. *Epigynum:* Resembles that in *Xenocytaea daviesae* new species in having anterior transverse arch, but lacks the posterior pocket; copulatory opening at the end of arch and not hidden under it, spermathecae globular (Figs. 103, 104).

Material examined.—**FIJI**: *Viti Levu,* Namosi District, hill forest on Namosi Road, about 7 km N of Queen's Road, 1♂ (holotype), 19 May 1987 (JWB & ERB). Tholo-I-Suva Forest Park, sweeping & shaking trees, 2♂1♀, 6 May 1987 (ERB).

Distribution.—Known only from Viti Levu, Fiji.

Xenocytaea zabkai new species
Figs. 105–107; Map 5

Holotype.—Holotype female from Fiji, Viti Levu, hill forest about 8 miles NE of Navua, tree sweeping and shaking, 2 May 1987 (J.W. & E.R. Berry) (BPBM).

Etymology.—The specific name is after Marek Żabka, Zaklad Zoologi, Siedlce, Poland, author of a number of papers on Salticidae.

Diagnosis.—Epigynal arch deeply concave, its margin not sinuous, widely separated from posterior pocket (Fig. 106).

Description.—*Female:* (*n* = 1). Total length 3.7, length of carapace 1.7, maximum carapace width 1.3, eye field length 1.0, eye row I width 1.2. Cephalothorax uniformly brown with dark brown eye field and lighter spot behind, with a few indistinct whitish adpressed setae, a few orange setae below PLE. Frontal aspect yellow, with anterior eyes surrounded with distinct whitish setae, clypeus almost bare below AME but with three curved bristles, with sparse whitish setae below ALE. Labium and sternum brown, endites lighter brown, coxae whitish. Abdominal pattern resembling *Xenocytaea maddisoni,* but more variegated (Fig. 105), posterior white diamond-shaped area smaller. Abdomen whitish with grey spot in front of spinnerets; spinnerets yellowish-grey surrounded by black. *Legs:* Legs and pedipalps whitish, distal segments slightly darker, with sparse short dark setae. Leg formula 4–3–1=2; patella-tibia III=IV. Patella-tibia I length 1.0. *Epigynum:* Resembles *Xenocytaea daviesae* by anterior transverse arch, copulatory openings hidden under the arch, spermathecae duct-like and curved, but running different course than in other species (Figs. 106, 107).

Male: The male is unknown.

Material examined.—Only the holotype.

Distribution.—Known only from Viti Levu, Fiji.

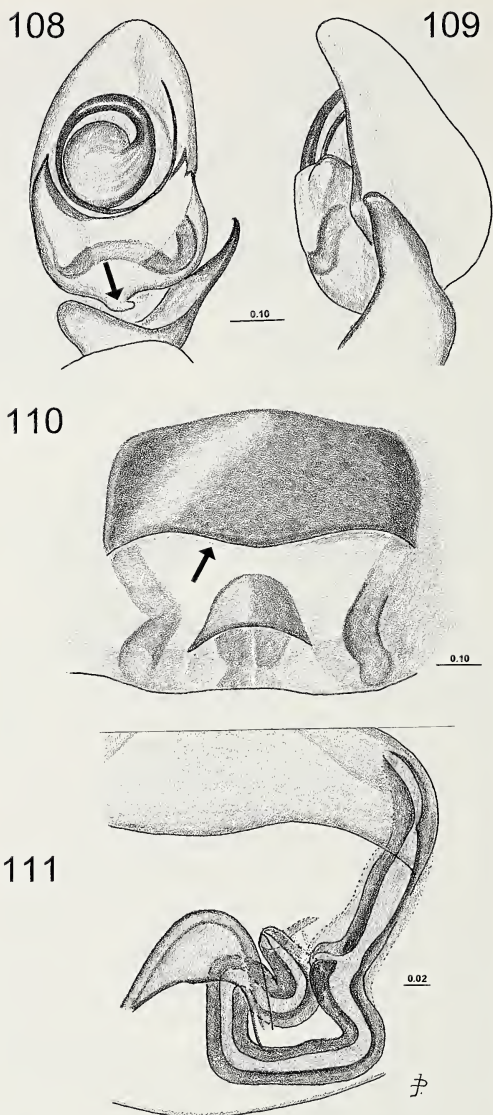### *Xenocytaea daviesae* new species
Figs. 108–111; Map 5

Holotype.—Holotype male from Fiji, Viti Levu, Nandarivatu, near swimming pool (stream) at Forestry Station, 14 May 1987 (J.W. & E.R. Berry) (BPBM).

Etymology.—The specific name, *daviesae,* is in honor of Valerie Todd Davies of the Queensland Museum, Australia, co-author of a major work on salticids of Australia (Davies & Żabka 1989).

Diagnosis.—The blunt hook on basal margin of male palpal bulb (Fig. 108) and the sinuous margin of the anterior epigynal arch (Fig. 110) distinguish *daviesae* from other species of the genus.

Description.—*Male:* (*n* = 1). Total length 3.2; length of carapace 2.1; maximum cara-

Figures 108–111.—*Xenocytaea daviesae* new species from Viti Levu, Fiji. 108, Holotype male, palp ventrally, with arrow indicating blunt hook on base of bulb; 109, Holotype male, palp laterally; 110, Epigynum, with arrow indicating anterior epigynal arch; 111, Internal structure of epigynum, showing left spermatheca and ducts.

pace width 1.3; eye field length 1.1; eye row I width 1.2. Frontal aspect light brown, with anterior eyes indistinctly surrounded with whitish setae, clypeus appearing bare. Chelicerae yellow, their anterior surface rounded. Pedipalps and metatarsus, tibia, patella and apical half of femur I dark olive grey, basal third of ventral surface of femur I whitish.

Cephalothorax almost uniformly brown, eye field with white adpressed setae, short group of whitish-orange setae stretches behind AME along ¼ of eye field; a few white setae behind PLE, and in semilunar transverse stripe across thoracic slope. Lower sides with sparse black setae. Abdomen greyish, with lighter spotted marginal parts of dorsal surface, white median streak, bisected antero-medially by darker line. *Legs:* Olive grey, legs I darker with basal half of femora, dorsal surfaces of patellae II-IV, and apical halves of tibiae II-IV whitish; metatarsi and tarsi I-IV yellowish. Retrolateral surface of tibia I densely covered with long, dark setae. Leg formula 4–3–1–2, patella-tibia III=IV. Patella-tibia I length 1.1. *Palp:* Embolus makes a flat coil on the ventral, anterior surface of bulb; apophysis single, long, laterally lobe-shaped (Figs. 108, 109).

Female: (*n* = 1). Total length 4.2; length of carapace 2.1; maximum carapace width 1.5; eye field length 1.1; eye row I width 1.4. Cephalothorax almost uniformly brown, eye field with white adpressed setae, orange setae around PLE; whitish setae on thoracic region, thin and sparse. Abdomen with minute dark setae and a few white setae denser along marginal belt. Frontal aspect light brown, with anterior eyes surrounded with distinct whitish setae, clypeus yellowish, with sparse white hairs and three curved bristles. *Legs:* Legs whitish, distal segments slightly darker, with sparse short dark setae. Leg formula 4–3–1–2, patella-tibia III = IV. Patella-tibia I length 1.1. *Epigynum:* With anterior arch and posterior pockets as in *Xenocytaea zabkai* and *maddisoni,* but with margin of arch sinuous; copulatory openings hidden under the arch, spermathecae duct-like and curved (Figs. 110, 111).

Material examined.—FIJI: *Viti Levu,* Nandarivatu near swimming pool at Forestry Station, 1♂ (holotype), 14 May 1987 (JWB & ERB). Nausori Highlands Forest Preserve, Leveitoko Block, elev. 1500 ft., shaking/picking. 1♀, 27 May 1987 (JWB & ERB).

Distribution.—Known only from Viti Levu, Fiji.

Xenocytaea maddisoni new species
Figs. 112–115; Map 5

Holotype.—Holotype male from Fiji, Viti Levu, Nandarivatu, tree shaking in scrub, elev.
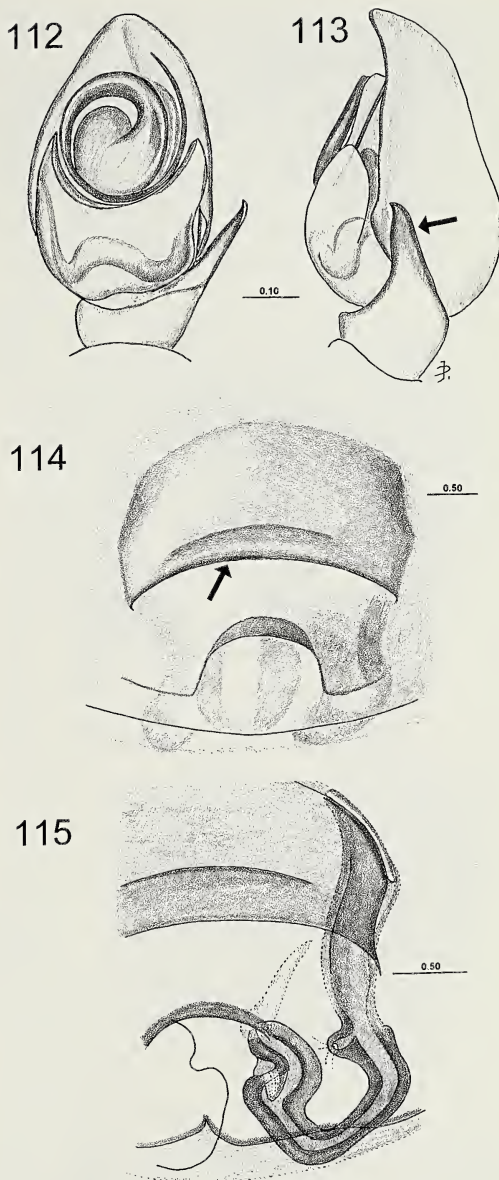
Figures 112–115.—*Xenocytaea maddisoni* new species from Viti Levu, Fiji. 112, Holotype male, palp ventrally; 113, Holotype male, palp laterally, with arrow indicating the narrow unbranched tibial apophysis; 114, Epigynum, with arrow indicating the semicircular arch; 115, Internal structure of epigynum, showing left spermatheca and ducts.

900 m, 11 April 1987 (J.W. & E.R. Berry (BPBM).

Diagnosis.—The combination of the semi-

circular non-sinuous arch of the epigynum lying close to the posterior pocket (Fig. 114), the absence of a basal hook on the male palpal bulb, and the narrow unbranched palpal tibial apophysis (Figs. 112, 113) separates this species from the rest of the genus. Patella, tibia and basal half of cymbium of male palp white.

Description.—*Male:* (*n* = 4). Total length 3.4–3.5 ($\bar{x}$ = 3.43), length of carapace 1.67–1.73 ($\bar{x}$ = 1.72), maximum carapace width 1.2–1.3 ($\bar{x}$ = 1.27), eye field length 0.9–1.0 ($\bar{x}$ = 0.97), eye row I width 1.17–1.20 ($\bar{x}$ = 1.19). Cephalothorax almost uniformly brown, with thin white adpressed setae, a few orange setae at lower rims of PLE; eye field blackish-brown. A bare area above a marginal row of white setae along the edge of cephalothorax. Labium dark brown, endites yellow, sternum brown, coxae whitish. Chelicerae brown, their anterior surface rounded. Frontal aspect light brown, anterior eyes surrounded with whitish setae, clypeus with small whitish setae. Abdomen with greyish-white pattern of four marginal grey areas separated by small white spots; a thin, white marginal line; median white streak along anterior half with yellow central area, separated from posterior half by grey and white chevrons; posterior area white with two triangular grey marginal spots posteriorly. *Legs:* Prolateral surface of tibia I with two spines (only one retrolaterally). A grey line extends over prolateral surfaces of metatarsus, tibia and patella I, apically along ventral surface of femur I; legs otherwise whitish, with short, sparse dark setae. Leg formula 4–3–1–2; patella-tibia III = IV. Patella-tibia I length 1.0–1.2 ($\bar{x}$ = 1.08). *Palp:* Resembles in shape and proportions that in *Xenocytaea daviesae* new species, but differs (Figs. 112–113) by the absence of a basal hook on the bulb.

Female: (*n* = 1). Total length 4.2, length of carapace 1.9, maximum carapace width 1.4, eye field length 1.0, eye row I width 1.2. Cephalothorax almost uniformly brown with white adpressed setae, a few orange setae below PLE. Abdominal pattern somewhat resembles male, with a pair of dark grey marginal areas at midlength, delimiting median light grey area with two pairs of indistinct grey spots arranged in two incomplete chevrons; posterior half of abdomen is light diamond-shaped area, delimited by dark. Marginal broad band of anterior half of abdomen

light, with sparse white scales. Labium dark brown, endites yellow, sternum brown, coxae whitish; abdomen whitish with large rectangular grey spot in the posterior half. Frontal aspect yellow, with anterior eyes surrounded with whitish setae, clypeus almost bare below AME but with three curved bristles, with sparse whitish setae under ALE. *Legs:* Legs (and pedipalps) whitish, distal segments slightly darker, with sparse short dark setae. Leg formula 4–3–1–2, patella-tibia III=IV. Patella-tibia I length 1.1. *Epigynum:* Resembling that in *Xenocytaea daviesae* new species by anterior transverse arch, copulatory openings hidden under the arch, spermathecae duct-like and curved (Figs. 114, 115).

Material examined.—**FIJI**: *Viti Levu,* Nandarivatu, tree shaking in scrub, elev. 900 m, 2♂ (including holotype) 1♀, 11 April 1987 (JWB & ERB). 22.4 km W of Suva City, forest sweeping & shaking, 1♂, 5 May 1987 (JWB & ERB). Namosi District, hilltop forest about 7 km N of Queen's Rd. on Namosi Road, 1♂, 19 May 1987 (JWB & ERB).

Distribution.—Known only from Fiji, Viti Levu.

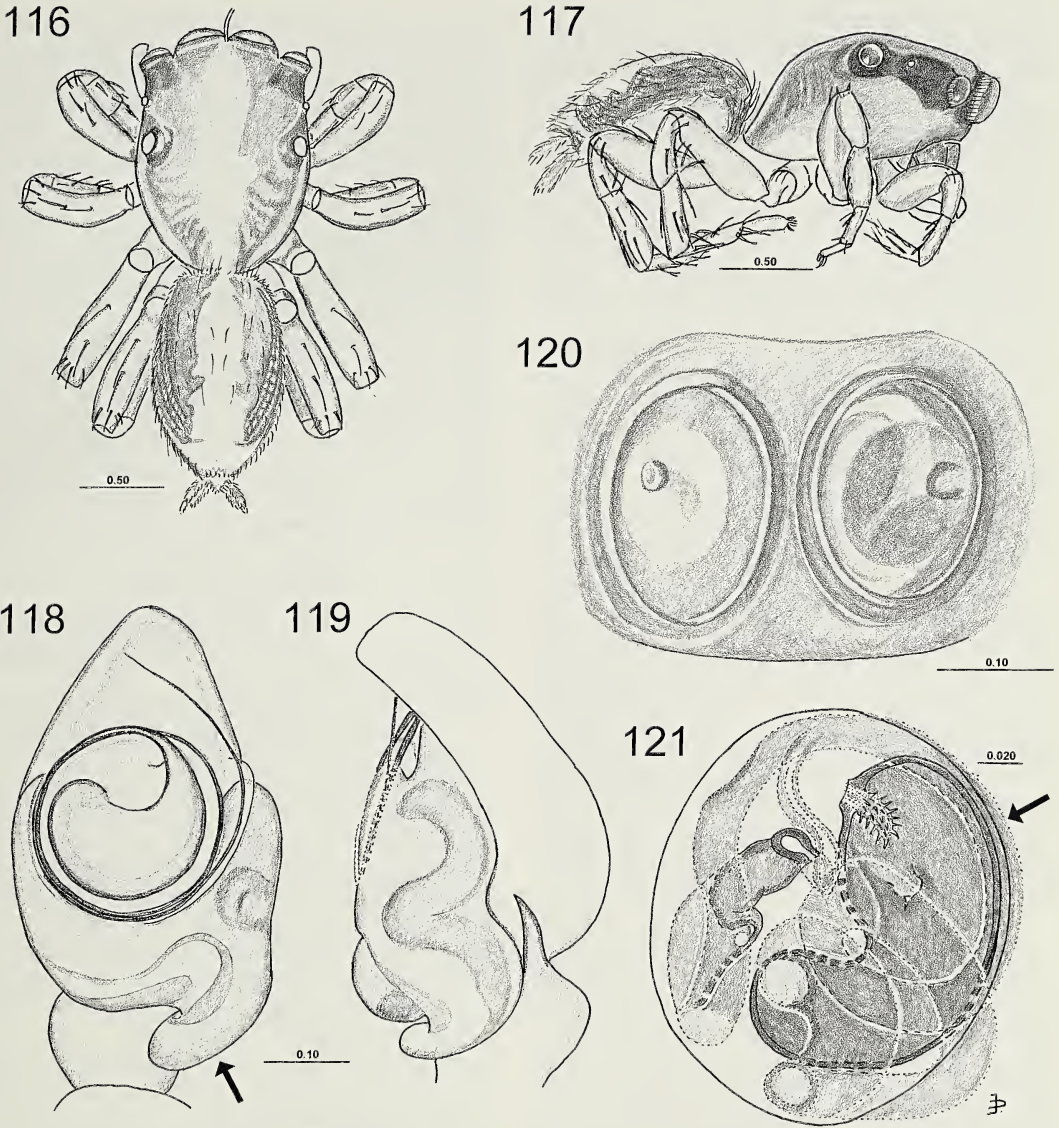### *Xenocytaea anomala* new species
Figs. 116–121, Map 5

Holotype.—Holotype male from Caroline Islands, Palau District, Pulo Anna Island, coconut litter, 7 April 1973 (J.W. & E.R. Berry) (BPBM).

Etymology.—The adjective *anomala* indicates the divergence of some characters of the species in comparison with others of the genus.

Diagnosis.—The epigynum differs from all other species of the genus by having large "windows," each spermatheca with ducts entirely framed by the "window" and lacking the arch and pocket. However, internal structures consist of similar elements as in the remaining species (Fig. 121). The extension of the palpal bulb beyond the cymbium retrolaterally and proximally (Figs. 118, 119) is distinctive.

Description.—General appearance of both sexes similar. Cephalothorax dark dorsally with distinct median streak of white adpressed setae, with indistinct darker lines radiating from the area of fovea; lower posterior sides pale yellow. Otherwise, eye field greyish-brown, covered with adpressed fawn setae; lower posterior sides pale yellow. Anterior eyes in a straight line. Anterior eyes surround-

Figures 116–121.—*Xenocytaea anomala* new species from Pulo Anna, Caroline Islands. 116, Holotype male, general appearance of male; 117, Holotype male, lateral view; 118, Palp of holotype ventrally, with arrow indicating extension of palpal bulb; 119, Palp of holotype, laterally; 120, Epigynum; 121, Internal structure of epigynum, showing left spermatheca and ducts.

ed with inconspicuous whitish-to-yellowish setae; PLE surrounded by black, also black pigmented spot behind ALE. Clypeus reduced; dorsal half of face darker; single row of sparse white setae along edge of clypeus (Fig. 117). Chelicerae yellow, suffused greyish in the middle, apically whitish-yellow. Abdomen with a broad, white median streak (Fig. 116), in some specimens divided by small dark chevrons, followed laterally by greyish-brown areas; posterior part of abdomen and sides pale yellow, ventrally pale yellow. *Legs:* Pedipalps yellowish-white. Anterior legs pale yellow, with dorsal surfaces slightly darker fawn. Leg formula 4–3–1–2; patella-tibia III=IV. Patella-tibia I length: males, 0.7–0.9 ($\bar{x}$ = 0.78); females, 0.8–0.9 ($\bar{x}$ = 0.85).

Male: (n = 5). Total length 2.7–3.0 ($\bar{x}$ = 2.86), length of carapace 1.3–1.4 ($\bar{x}$ = 1.35), maximum carapace width 0.97–1.03 ($\bar{x}$ =

0.99), eye field length 0.7–0.8 ($\bar{x}$ = 0.71), eye row I width 1.00–1.03 ($\bar{x}$ = 1.02). *Palp:* Bulb extending laterally and proximally beyond cymbium, prolonged retrobasally into a blunt curved extension overlapping the tibia. Embolus coiled flat on bulb, making two turns (see Figs. 118, 119).

Female: (n = 5). Total length 3.0–3.7 ($\bar{x}$ = 3.41), length of carapace 1.3–1.6 ($\bar{x}$ = 1.45), maximum carapace width 1.0–1.2 ($\bar{x}$ = 1.10), eye field length 0.7–0.8 ($\bar{x}$ = 0.78), eye row I width 1.07–1.13 ($\bar{x}$ = 1.10). *Epigynum:* Lacking the arch found in the other members of the genus; with two oval windows separated by a narrow septum, coils of ducts lie entirely dorsal to windows (Figs. 120, 121).

Material examined.—CAROLINE ISLANDS: *Palau,* Pulo Anna, 2♂ (including holotype) 2♀, 7 April 1973 (JWB & ERB). Sonsorol Is., forest litter, 1♂1♀ 1imm, 6 April 1973 (JWB & ERB). Kayangel Atoll, mixed coconut/*Barringtonia,* tree shaking, 1♀, 22 April 1973 (JWB & ERB). Kayangel Atoll, in cycad tree, 1♂ 1imm, 22 April 1973 (JWB). Babelthuap Is., Ngaremlengui village, grass field, sweeping, 1♂ 1imm, 21 April 1973 (JWB & ERB). Peleliu, tree shaking, 4♂ 3imm, 21 March 1973 (JWB & ERB). Angaur Is., *Casuarina* litter, 1♀, 30 April 1973 (JWB & ERB).

Distribution.—Known only from the Palau District, western Caroline Islands.

ACKNOWLEDGMENTS

LITERATURE CITED

Audouin, V. 1825. Explication sommaire des planches. Pp. (1):1–339. *In* Savigny, Description de l'Egypte.

Berland, L. 1929. Araignées (Araneida). Pp. 8:35–78. *In* Insects of Samoa and Other Samoan Terrestrial Arthropoda. London.

Berland, L. 1938. Araignées des Nouvelles-Hébrides. Annal. Soc. Entomol. France, 107:121–190.

Berland, L. & J. Millot. 1941. Les araignées de l'Afrique occidentale Francaise. I. Les Salticides. Mem. Mus. Nat. Hist. Nat. Paris (N.S.), 12:297–423.

Berry, J.W., J.A. Beatty & J. Prószyński. 1996. Salticidae of the Pacific islands. I. Distribution of twelve genera, with descriptions of eighteen new species. J. Arachnol., 24:214–253.

Berry, J.W., J.A. Beatty & J. Prószyński. 1997. Salticidae of the Pacific islands. II. Distribution of nine genera, with descriptions of eleven new species. J. Arachnol., 25:109–136.

Brignoli, P.M. 1983. A catalogue of the Araneae described between 1940 and 1981. Manchester. 775 pp.

Bonnet, P. 1957. Bibliographia Araneorum, 2:1927–3026. Toulouse.

Chrysanthus, Fr. 1968. Spiders from South New Guinea X. Tijdschrift voor Entomol., 111:49–74.

Clark, D.J. 1974. Notes on Simon's types of African Salticidae. Bull. British Arachnol. Soc., 3(1):11–27.

Davies, V.T. & M. Żabka. 1989. Illustrated keys to the jumping spiders (Araneae: Salticidae) in Australia. Mem. Queensland Mus., 27:189–266.

Doleschall, C. L. 1859. Tweede Bijdrage tot de Kennis der Arachniden van den Indischen Archipel. Act. Soc. Sci. Ind.-Neerlandicae, 5:1–60.

Dufour, L. 1831. Descriptions et figures de quelques

Arachnides nouvelles ou mal connues. . . Annal. Sci. Nat. Zool., 22:355–371.

Keyserling, E. 1882. Die Arachniden Australiens. . . Nürnberg. Pp.1325–1420.

Koch, L. 1867. Beschreibungen neuer Arachniden und Myriapoden. Verh. Zool-bot. Ges. Wien, 17: 173–250.

Maddison, W. 1987. *Marchena* and other jumping spiders with an apparent leg-carapace stridulatory mechanism (Araneae: Salticidae: Heliophaninae and Thiodininae). Bull. British Arachnol. Soc., 7:101–106.

Maddison, W. 1996. *Pelegrina* Franganillo and other jumping spiders formerly placed in the genus *Metaphidippus*. Bull. Mus. Comp. Zool., 154: 215–368.

Marples, B.J. 1957. Spiders from some Pacific islands. II. Pacific Sci., 11:386–395.

Marples, B.J. 1964. Spiders from some Pacific Islands, Part V. Pacific Sci., 18:399–410.

Prószyński, J. 1984. Atlas rysunkow diagnostycznych mniej znanych Salticidae. Zesz. Naukowe WSRP, Siedlce. Part 1. 177 pp.

Prószyński, J. 1987. Atlas rysunkow diagnostycznych mniej znanych Salticidae. Zesz. Naukowe WSRP, Siedlce. Part 2. 172 pp.

Prószyński, J. 1990. Catalogue of Salticidae (Araneae). Wyższa Szkola Rolniczo-Pedagogiczna w Siedlcach. Siedlce (Poland). 366 pp. (Version 1998 available at http://spiders.arizona.edu/salticid/catalog/0-tit-pg.htm)

Prószyński, J. 1992. Salticidae (Araneae) of the Old World and Pacific Islands in several U.S. collections. Annal. Zool. Warszawa, 44:87–163.

Simon, E. 1868. Monographie des espècies euro-péenes de la famille des Attidae. Annal. Soc. Entomol. France, (4) 8:529–726.

Simon, E. 1871. Revésion des Attidae européens. Annal. Soc. Entomol. France, (5) 1:329–360.

Simon, E. 1885a. Matériaux pour servir á la faune arachnologique de l'Asie meridionale. Bull. Soc. Zool. France, 10:1–139.

Simon, E. 1885b. Etudes sur les Arachnides recueillis en Tunisie en 1883 et 1884 . . . *In* Exploration scientifique de la Tunisie. Paris.

Simon, E. 1897. Etudes arachnologiques. 28e Memoire. XLIII. Arachnides recueillis par M. le Dr. Ph. François en Nouvelle-Calédonie, aux Nouvelle-Hébrides (Mallicolo) et à l'ile de Vanikoro. Annal. Soc. Entomol. France, 66:271–276.

Simon, E. 1901. Histoire Naturelle des Araignées. Tome 2, fasc. 3, Pp. 381–668. Paris.

Simon, E. 1903. Histoire Naturelle des Araignées. Tome 2, fasc. 4, Pp. 669–1080. Paris.

Thorell, T. 1878. Studi sui Ragni Malesi e Papuani. Part II. Annal. Mus. Civ. Stor. Nat. Genova, 13: 1–317.

Thorell, T. 1881. Studi sui Ragni Malesi e Papuani. Part III. Ragni di Amboina raccolti dal Prof. O. Beccari. Annal. Mus. Civ. Stor. Nat. Genova, 17: 1–720.

Wanless, F. 1978. A revision of the spider genus *Sobasina* (Araneae: Salticidae). Bull. British Mus. Nat. Hist. (Zool.), 33:245–257.

Żabka, M. 1993. Salticidae (Arachnida: Araneae) of the Oriental, Australian and Pacific Regions. IX. Genera *Afraflacilla* Berland & Millot 1941 and *Evarcha* Simon 1902. Rec. West Australian Mus., 15:673–84.

THE EFFECTS OF ORGANIC FARMING ON SURFACE-ACTIVE SPIDER (ARANEAE) ASSEMBLAGES IN WHEAT IN SOUTHERN ENGLAND, UK

R.E. Feber[1, 3], **J. Bell**[1, 4], **P.J. Johnson**[1], **L.G. Firbank**[2] and **D.W. Macdonald**[1]: [1]Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK; and [2]Institute of Terrestrial Ecology, Merlewood Research Station, Grange-over-Sands, Cumbria LA11 GJU, UK

ABSTRACT. Spiders were sampled from organically farmed and conventionally farmed winter wheat fields at three sites in southern England, UK, using pitfall traps. A range of vegetation variables was also recorded from each field. We identified 56 species of spiders from 8609 individuals in our study samples. Most species caught belong to the Linyphiidae, with especially high captures of *Oedothorax* spp., *Erigone* spp., *Lepthyphantes tenuis* (Blackwall 1852), *Bathyphantes gracilis* (Blackwall 1841) and *Meioneta rurestris* (C.L. Koch 1836). The Lycosidae were also well represented by *Pardosa* and *Trochosa* spp., although the samples were largely dominated by the presence of *Pardosa palustris* (Linnaeus 1758). More spiders, and more species of spiders, were captured from organic than from conventional fields. Principal Component Analyses suggested that the spider communities differed between the contrasting systems. Our results showed that more spiders, and a greater number of spider species, were captured with increasing abundance of understory vegetation within the crop, both overall and within each farming system.

The intensification of arable agriculture over the last 50 years has been associated with substantial losses of biodiversity (Potts 1991; Gibbons et al. 1993; Firbank et al. 1994; Stewart et al. 1994). Several factors have been implicated, including loss of habitat (e.g., Moore 1962; Webb 1990), the direct and indirect effects of pesticides and herbicides (e.g., Newton & Wyllie 1992; Potts & Aebischer 1991), increased use of drainage and inorganic fertilizers (Fuller 1987), the loss and degradation of field boundary features (Barr et al. 1993) and changing patterns of cropping (Gibbons et al. 1993). Over the last ten years or so, there has been an increased awareness of environmental, health and amenity aspects of agriculture which, together with the need to reduce food surpluses within the European Union during the 1980s, has led to an increase in interest in low-input and organic agriculture. Such farming systems tend to be less productive in terms of yield per hectare than high-input systems, but this can be outweighed by savings on inputs and by improved product quality and environmental benefits (Lampkin 1990; El Titi 1991; Jordan & Hutcheon 1995). For example, results from the Boxworth Project showed that reduction in pesticide use had a number of positive effects on the invertebrate fauna of arable fields (Grieg-Smith et al. 1991).

In this paper we present data on spider (Araneae) assemblages in cereal crops on three pairs of organic and conventional farms in southern England, UK. Spiders are increasingly studied in agroecosystems because they are recognized as a significant component of the polyphagous complex (Sunderland et al. 1986; Young & Edwards 1990). Spiders have been shown to be useful in controlling aphid increase (DeClercq & Pietraszko 1983) particularly in spring and early summer (Alderweireldt 1994; Sunderland et al. 1986) when aerial activity is at a peak (Bishop 1990; Bishop & Riechert 1990) and the initial population of aphids can be restrained.

The success of spiders as biocontrol agents depends on the type and duration of management practices within each field (Riechert & Lockley 1984). Annual plowing results in a

[3]Current address: CABI Biosciences UK Centre (Ascot), Silwood Park, Ascot, Berks. 5L5 7TA, UK.
[4]Current address: Manchester Metropolitan Univ., Dept. of Environmental and Geographical Sciences, John Dalton Building, Chester Street, Manchester, M1 5GD, UK.

reduced spider diversity (Haskins & Shaddy 1986); and pesticides, although not always seen as disruptive (Riechert & Lockley 1984), can decrease the spider population size for more than a month after application (Clausen 1990). However, not all agricultural practices exert a negative impact on spider communities. The introduction of legume species for pasture improvement using tillage practices, for example, can maintain the fields' spider communities because disturbance is kept to a minimum (Mangan & Byers 1989). Furthermore, irrigation of a crop once it has been established can increase the quality of habitat for lycosid spiders due to the larger plant canopy (Agnew & Smith 1989).

Organic farming systems are the extreme expression of low-input agriculture in the UK. Such systems could potentially sustain larger or more diverse spider communities than more intensive farming systems because of the absence of agrochemical use and the typically more complex crop rotations within the system. For example, Gluck & Ingrish (1990) showed that intensively farmed fields had fewer spider species, and lower activity of Lycosidae, than bio-dynamic fields. Our study aimed to characterize the spider communities of organic and conventional winter wheat fields in southern England, UK, and quantify any differences which might exist between the spider assemblages of the two systems. We discuss the implications of any differences for spider conservation in contrasting arable systems.

METHODS

The study was conducted on three pairs of organic and conventionally managed farms in southern England, UK. Two sites were in Gloucestershire (Broadfield, ST8895, and Harnhill, SP 0702) and one was in Oxfordshire (North Aston, SP4799). All fields were in winter wheat. Organic and conventional fields at any one site were located close together to minimize variations in soil type. Spiders were sampled in three organic and three conventional fields at each site, using pitfall trapping. Although experiments have shown that pitfall trap catches can be affected by a number of factors such as differing activity rates and habitat structure (Topping 1993; Topping & Sunderland 1992), pitfall trapping is nonetheless a valuable and widely used

method of investigating the activity of surface-dwelling invertebrates (e.g., Luff & Eyre 1988; Merrett & Snazell 1983), as long as the results are interpreted in terms of catch size and composition rather than mean densities.

Pitfall trapping was conducted at the end of May and the end of June in 1995. Twelve pitfall traps (plastic cups of 7 cm diameter, 8 cm deep) were placed in a grid formation in each of the 18 fields under study, with traps approximately 24 m apart. Each trap was set with a 70% ethylene glycol solution and was emptied after 10 days. No traps were lost or flooded. The samples were stored in a 70% ethanol solution during sorting and identification to species level. Nomenclature follows Roberts (1987). Voucher specimens from the study have been deposited at the University Museum, Parks Road, Oxford, UK (Organic Farming Collection).

Vegetation was sampled at the same time as each pitfall session. Quadrats, 0.5 m², were placed adjacent to each of the 216 pitfall traps. We recorded the number of crop stems, crop height, and percentage cover of non-crop grasses, non-woody broad-leaved species, leaf litter and bare ground within each quadrat. For the purposes of analysis, the sample units within individual fields were amalgamated to give a single data point for each field on each sample date.

Data analysis.—We used SAS software for all analyses (SAS Institute 1988). In the analysis for testing for organic versus conventional differences, simple two-way ANOVAs were used (SAS PROC GLM). Sites were treated as blocks, and the fields as replicates of the management systems within the sites.

Comparison of organic and conventional effects: The standard method of analysis for designs of this format, with a fixed effect (management system) replicated within a random effect (site) is a mixed model ANOVA using the interaction mean square as the denominator for the fixed effect. However, as McKone & Lively (1993) point out, this approach has low power in detecting a general treatment effect where few sites are sampled. Here, where we sampled only three sites, we adopted an alternative analysis suggested by these authors and applied an analysis with treatment nested within site. It should be noted that significant treatment effects in this

Table 1.—Total abundance of each species recorded from samples taken in May. Proportion of sample formed by each species from indicated field types and sites given in parentheses.

Species	Broadfield		Harnhill		North Aston	
	Conven-tional	Organic	Conven-tional	Organic	Conven-tional	Organic
Thomisidae						
Xysticus cristatus (Clerck 1757)	0 (0)	0 (0)	1 (0.00)	6 (0.01)	0 (0)	0 (0)
Ozyptila praticola (C.L.K. 1837)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0.00)
Lycosidae						
Pardosa palustris (Linn. 1758)	2 (0.02)	16 (0.14)	115 (0.37)	167 (0.35)	32 (0.04)	5 (0.02)
P. pullata (Clerck 1757)	0 (0)	0 (0)	1 (0.00)	3 (0.01)	1 (0.00)	0 (0)
P. prativaga (L.K. 1870)	3 (0.03)	2 (0.02)	7 (0.02)	11 (0.02)	3 (0.00)	16 (0.05)
P. amentata (Clerck 1757)	3 (0.03)	1 (0.01)	1 (0.00)	1 (0.00)	0 (0.00)	0 (0)
Trochosa ruricola (Deg. 1778)	4 (0.04)	0 (0)	0 (0.00)	6 (0.01)	3 (0.00)	1 (0.00)
T. terricola Thor. 1856	0 (0)	1 (0.01)	0 (0.00)	0 (0)	0 (0)	0 (0)
Pisauridae						
Pisaura mirabilis (Clerck 1757)	0 (0)	0 (0)	0 (0)	1 (0.00)	0 (0)	0 (0)
Tetragnathidae						
Pachygnatha clercki Sund. 1823	0 (0)	0 (0)	0 (0)	0 (0.00)	0 (0)	10 (0.03)
P. degeeri Sund. 1830	2 (0.02)	3 (0.03)	22 (0.07)	18 (0.04)	13 (0.02)	0 (0)
Linyphiidae						
Ceratinella brevipes (West. 1851)	0 (0)	0 (0)	1 (0.00)	0 (0)	0 (0)	0 (0)
Walckenaeria nudipalpis (West. 1851)	0 (0)	0 (0)	1 (0.00)	1 (0.00)	0 (0)	4 (0.01)
W. vigilax (Bl. 1853)	0 (0)	0 (0)	6 (0.02)	2 (0.00)	1 (0.00)	0 (0)
W. antica (Wid. 1834)	0 (0)	0 (0)	0 (0.00)	1 (0.00)	0 (0.00)	0 (0)
Dicymbium nigrum (Bl. 1834)	0 (0)	0 (0)	0 (0.00)	1 (0.00)	0 (0)	1 (0.00)
Dismodicus bifrons (Bl. 1841)	0 (0)	1 (0.01)	0 (0)	0 (0)	0 (0)	0 (0)
Pocadicnemis juncea L. & M. 1953	1 (0.01)	0 (0)	0 (0)	0 (0)	1 (0.00)	0 (0)
Oedothorax fuscus (Bl. 1834)	0 (0)	1 (0.01)	0 (0)	2 (0.00)	94 (0.11)	3 (0.01)
O. retusus (West. 1851)	1 (0.01)	1 (0.01)	6 (0.02)	2 (0.00)	4 (0.00)	7 (0.02)
O. apicatus (Bl. 1850)	0 (0)	0 (0)	11 (0.04)	17 (0.04)	5 (0.01)	1 (0.00)
Troxochrus scabriculus (West. 1851)	0 (0)	0 (0)	0 (0)	1 (0.00)	0 (0)	0 (0)
Gongylidiellum vivum (Camb. 1875)	1 (0.01)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Micrargus subaequalis (West. 1851)	0 (0)	1 (0.01)	0 (0)	0 (0)	2 (0.00)	0 (0)
Savigna frontata (Bl. 1833)	5 (0.05)	1 (0.01)	5 (0.02)	2 (0.00)	2 (0.00)	6 (0.02)
Diplocephalus latifrons (Camb. 1863)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0.00)
Araeoncus humilis (Bl. 1841)	0 (0)	0 (0)	0 (0)	2 (0.00)	0 (0)	0 (0)
Milleriana inerrans (Camb. 1885)	7 (0.07)	34 (0.29)	3 (0.01)	15 (0.03)	34 (0.04)	4 (0.01)
Erigone dentipalpis (Wid. 1834)	3 (0.03)	3 (0.03)	3 (0.01)	20 (0.04)	175 (0.21)	8 (0.03)

Table 1.—Continued.

Species	Broadfield		Harnhill		North Aston	
	Conventional	Organic	Conventional	Organic	Conventional	Organic
E. atra Bl. 1833	35 (0.35)	24 (0.21)	63 (0.20)	148 (0.31)	403 (0.48)	188 (0.63)
E. promiscua (Camb. 1872)	1 (0.01)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Halorates distinctus (Sim. 1884)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0.00)
Porrhomma pygmaeum (Bl. 1834)	1 (0.01)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
P. microphthalmum (Camb. 1871)	1 (0.01)	4 (0.03)	3 (0.01)	4 (0.01)	1 (0.00)	3 (0.01)
Meioneta rurestris (C.L.K. 1836)	2 (0.02)	6 (0.05)	2 (0.01)	12 (0.03)	9 (0.01)	6 (0.02)
Bathyphantes gracilis (Bl. 1841)	5 (0.05)	4 (0.03)	22 (0.07)	17 (0.04)	22 (0.03)	11 (0.04)
Diplostyla concolor (Wid. 1834)	2 (0.02)	0 (0)	0 (0)	0 (0)	0 (0)	7 (0.02)
Lepthyphantes tenuis (Bl. 1852)	22 (0.22)	14 (0.12)	37 (0.12)	10 (0.02)	28 (0.03)	13 (0.04)
Linyphia hortensis Sund. 1830	0 (0)	0 (0)	0 (0)	1 (0.00)	0 (0)	0 (0)
Neriene clathrata (Sund. 1830)	0 (0)	0 (0)	0 (0)	1 (0.00)	0 (0)	0 (0)
Allomenga scopigera (Grube 1859)	0 (0)	0 (0)	1 (0.00)	0 (0.00)	0 (0)	0 (0)

analysis cannot be generalized to the wider population of sites.

Community analyses: To detect patterns in the species composition of the spider assemblages at each of the two sample dates, we used Principal Components Analysis (PCA) on the standardized species-sample matrices (SAS PROC FACTOR). PCA is a data reduction technique which allows patterns in a multivariate data set to be represented in a lower dimensional space (Pielou 1984). The method derives new axes (components) of variation in the data-set which summarize as much of the variation in the original data as possible. Hence the location of samples on biplots of their scores on these derived axes is related to their spider species composition. Samples with similar compositions appear closer together. Species abundances were log $(x + 1)$ transformed to improve normality. Only species found in nine or more of the 18 samples in each analysis were included.

Vegetation variables: To relate the vegetation data to the size and composition of spider catches, the non-independence of samples within fields and fields within sites was first eliminated from both variable sets using hierarchical regression. This generated residual values free of site and field co-variation. Simple correlation analysis was then used to estimate the degree of relationship between these residuals. This is exactly equivalent to Stearns' phylogenetic subtraction method for investigating relationships between life history characteristics independent of phylogeny (Harvey & Pagel 1991).

RESULTS

Spider assemblages.—We identified 56 species from 8609 individuals in our study samples (Tables 1, 2). Most species caught belong to the family Linyphiidae and are commonly recorded on agricultural land in the UK. (Alderweireldt 1994; Topping & Sunderland 1994), with high captures of *Oedothorax* spp., *Erigone* spp., *Lepthyphantes tenuis* (Blackwall 1852), *Bathyphantes gracilis* (Blackwall 1841) and *Meioneta rurestris* (C.L. Koch 1836). The Lycosidae were well represented by *Pardosa* and *Trochosa* spp., although the samples were largely dominated by the presence of *Pardosa palustris* (Linnaeus

Table 2.—Total abundance of each species recorded from samples taken in June. Proportion of sample formed by each species from indicated field types and sites given in parentheses.

Species	Broadfield		Harnhill		North Aston	
	Conventional	Organic	Conventional	Organic	Conventional	Organic
Clubionidae						
Clubiona reclusa Camb. 1863	0 (0)	1 (0.00)	0 (0)	0 (0)	0 (0)	0 (0)
C. terrestris West. 1851	0 (0)	1 (0.00)	0 (0)	0 (0)	0 (0)	0 (0)
Thomisidae						
Xysticus cristatus (Clerck 1757)	1 (0.00)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Tibellus oblongus (Walck. 1802)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0.00)	0 (0)
Lycosidae						
Pardosa palustris (Linn. 1758)	1 (0.00)	7 (0.02)	107 (0.08)	58 (0.07)	20 (0.01)	0 (0)
P. pullata (Clerck 1757)	1 (0.00)	2 (0.00)	0 (0)	0 (0)	1 (0)	0 (0)
P. prativaga (L.K. 1870)	1 (0.00)	1 (0.00)	1 (0.00)	0 (0)	0 (0)	2 (0.00)
P. amentata (Clerck 1757)	3 (0.01)	3 (0.01)	0 (0)	0 (0)	1 (0.00)	0 (0)
Trochosa ruricola (Deg. 1778)	1 (0.00)	0 (0)	2 (0.00)	0 (0)	2 (0.00)	0 (0)
T. terricola Thor. 1856	0 (0)	1 (0.00)	0 (0)	0 (0)	0 (0)	0 (0)
Pisauridae						
Pisaura mirabilis (Clerck 1757)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0.00)
Agelenidae						
Tetrix denticulata (Oliv. 1789)	0 (0)	0 (0)	0 (0)	2 (0.00)	0 (0)	0 (0)
Theridiidae						
Robertus neglectus (Camb. 1871)	0 (0)	0 (0)	2 (0.00)	0 (0)	0 (0)	0 (0)
Tetragnathidae						
Pachygnatha degeeri Sund. 1830	1 (0.00)	0 (0)	6 (0.00)	0 (0)	7 (0.00)	0 (0)
Linyphiidae						
Walckenaeria nudipalpis (West. 1851)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (0.00)
W. vigilax (Bl. 1853)	2 (0.00)	1 (0.00)	7 (0.01)	23 (0.03)	2 (0.00)	0 (0)
W. atrotibialis (Camb. 1878)	0 (0)	0 (0)	2 (0.00)	0 (0)	1 (0.00)	0 (0)
Oedothorax fuscus (Bl. 1834)	53 (0.10)	86 (0.19)	48 (0.04)	66 (0.08)	478 (0.24)	25 (0.06)
O. retusus (West. 1851)	16 (0.03)	44 (0.10)	37 (0.03)	39 (0.05)	171 (0.09)	18 (0.04)
O. apicatus (Bl. 1850)	16 (0.03)	13 (0.03)	606 (0.47)	285 (0.34)	101 (0.05)	29 (0.07)
Troxochrus scabriculus (West. 1851)	0 (0)	0 (0)	0 (0)	2 (0.00)	0 (0)	0 (0)
Gongylidiellum vivum (Camb. 1875)	1 (0.00)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Micrargus subaequalis (West. 1851)	1 (0.00)	2 (0.00)	0 (0)	0 (0)	0 (0)	0 (0)
Erigonella hiemalis (Bl. 1841)	1 (0.00)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Savigna frontata (Bl. 1833)	2 (0.00)	0 (0)	2 (0.00)	0 (0)	8 (0.00)	1 (0.00)
Diplocephalus cristatus (Bl. 1833)	0 (0)	0 (0)	0 (0)	2 (0.00)	0 (0)	0 (0)

Table 2.—Continued.

Species	Broadfield		Harnhill		North Aston	
	Conven-tional	Organic	Conven-tional	Organic	Conven-tional	Organic
Araeoncus humilis (Bl. 1841)	0 (0)	0 (0)	1 (0.00)	0 (0)	0 (0)	0 (0)
Milleriana inerrans (Camb. 1885)	24 (0.05)	15 (0.03)	1 (0.00)	19 (0.02)	98 (0.05)	3 (0.01)
Erigone dentipalpis (Wid. 1834)	30 (0.06)	6 (0.01)	2 (0)	14 (0.02)	209 (0.10)	22 (0.05)
E. atra Bl. 1833	220 (0.42)	75 (0.16)	223 (0.17)	172 (0.2)	737 (0.37)	208 (0.50)
E. longipalpis (Sund. 1830)	0 (0)	0 (0)	0 (0)	0 (0)	3 (0.00)	0 (0)
Leptorhoptrum robustum (West. 1851)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0.00)	0 (0)
Porrhomma oblitum (Camb. 1871)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0.00)
P. microphthalmum (Camb. 1871)	0 (0)	1 (0.00)	0 (0)	0 (0)	2 (0.00)	3 (0.01)
Agyneta sublitis (Camb. 1863)	0 (0)	0 (0)	2 (0.00)	0 (0)	0 (0)	0 (0)
A. decora (Camb. 1871)	0 (0)	0 (0)	0 (0)	0 (0)	4 (0.00)	0 (0)
Meioneta rurestris (C.L.K. 1836)	82 (0.16)	107 (0.23)	84 (0.07)	121 (0.14)	60 (0.03)	14 (0.03)
M. saxatilis (Bl. 1844)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0.00)	0 (0)
Saaristoa abnormis (Bl. 1841)	1 (0.00)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Bathyphantes gracilis (Bl. 1841)	14 (0.03)	13 (0.03)	23 (0.02)	4 (0)	36 (0.02)	37 (0.09)
Diplostyla concolor (Wid. 1834)	1 (0.00)	1 (0.00)	0 (0)	0 (0)	1 (0.00)	0 (0)
Lepthyphantes tenuis (Bl. 1852)	51 (0.10)	76 (0.17)	127 (0.10)	34 (0.04)	55 (0.03)	53 (0.13)

1758), a common predator in wheat fields (Nyffeler & Benz 1988). Three uncommon spider species were also captured during the study: *Robertus neglectus* (O.P.-Cambridge 1871) (Theridiidae), *Halorates distinctus* (Simon 1884) (Linyphiidae) and *Porrhomma oblitum* (O.P.-Cambridge 1871) (Linyphiidae). *H. distinctus* is associated with very damp environments, and the rare *P. oblitum* is thought to be subterranean, making small webs within the cracks in the soil (Roberts 1987).

Species restrictions.—When both sampling dates were combined, three species were captured only in organically farmed fields. These were *Diplocephalus cristatus* (Blackwall 1833) (Linyphiidae), *Tetrix denticulata* (Olivier 1789) (Agelenidae) and *Pachygnatha clercki* (Sundevall 1823) (Tetragnathidae). Five different species, *Agyneta subtilis* (O.P.-Cambridge 1863) (Linyphiidae), *Agyneta decora* (O.P.-Cambridge 1871) (Linyphiidae), *Gongylidiellum vivum* (O.P.-Cambridge 1875)

(Linyphiidae), *Erigone longipalpis* (Sundevall 1830) (Linyphiidae) and *R. neglectus* were captured exclusively in conventionally farmed fields. However, none of these eight species was caught at more than one site.

Catch size.—In late May, more spiders were caught on all three organic farms than on all three conventional farms. In the nested analysis this was significant only for North Aston ($F_{(1, 12)} = 9.5$, $P < 0.01$; Fig. 1). In late June, spider catches were larger at all sites. As in May, significantly more spiders were caught on the organic fields than the conventional fields at North Aston ($F_{(1, 12)} = 25.9$, $P = 0.001$; Fig. 1). Spider catches were larger on conventional than organic fields in June at the two other sites, although this was non-significant (Fig. 1).

Catch composition.—More species of spider were captured on organic than on conventional fields in late May; this effect was significant for the North Aston site ($F_{(1, 12)} =$
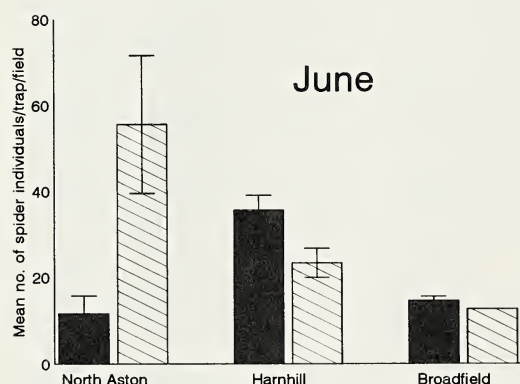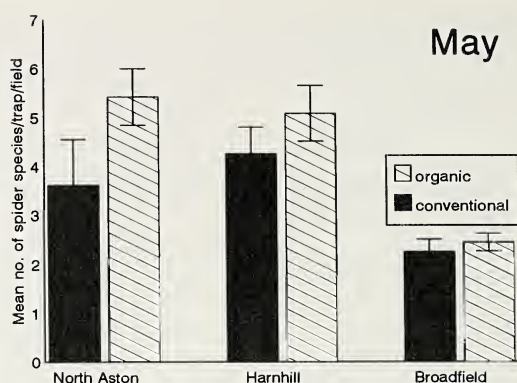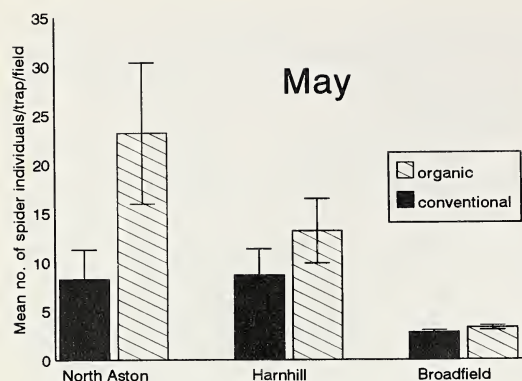
Figure 1.—Mean number of spider individuals caught per trap per field on organic and conventional fields at three sites in May and June.

Figure 2.—Mean number of spider species caught per trap per field on organic and conventional fields at three sites in May and June.

5.24, $P < 0.05$; Fig. 2). In June, significantly more species were again captured on organic fields at North Aston ($F_{(1, 12)} = 39.0$, $P < 0.001$), but catch composition was very similar between both systems at the other sites (Fig. 2).

Community results.—The Principal Components Analysis for the May sample summarized 47% of the overall variance in species abundance between the samples on the first two derived axes. A biplot of the location of the samples suggested that there were differences in the spider species composition both between sites and, within sites, between management systems (Fig. 3a). At the North Aston site the organic samples scored more highly on both axes, while at Harnhill organic samples were higher on the second axis alone. At Broadfield the organic samples scored highly on only the first axis. Inspection of the factor pattern for these axes revealed that the first

axis was principally related to the high capture of the species *P. palustris*, *B. gracilis*, *Pachygnatha degeeri* (Sundevall 1823) (Tetragnathidae), and *Oedothorax apicatus* (Blackwall 1850) (Linyphiidae) (loadings of 0.91, 0.54, 0.91 and 0.88, respectively). Highest loadings on the second axis were for *Erigone atra* (Blackwall 1833) (Linyphiidae), *Erigone dentipalpis* (Wider 1834) (Linyphiidae) and *Oedothorax fuscus* (Blackwall 1834) (Linyphiidae) (loadings of 0.76, 0.94 and 0.90, respectively).

The equivalent analysis for the June samples summarized 59% on the first two axes. In this sample round, the clearest resolution between sites and management systems was achieved with axes one and three (Fig. 3b). There was a tendency for organic samples from all sites to score higher on the first axis, and lower on the third, by comparison with
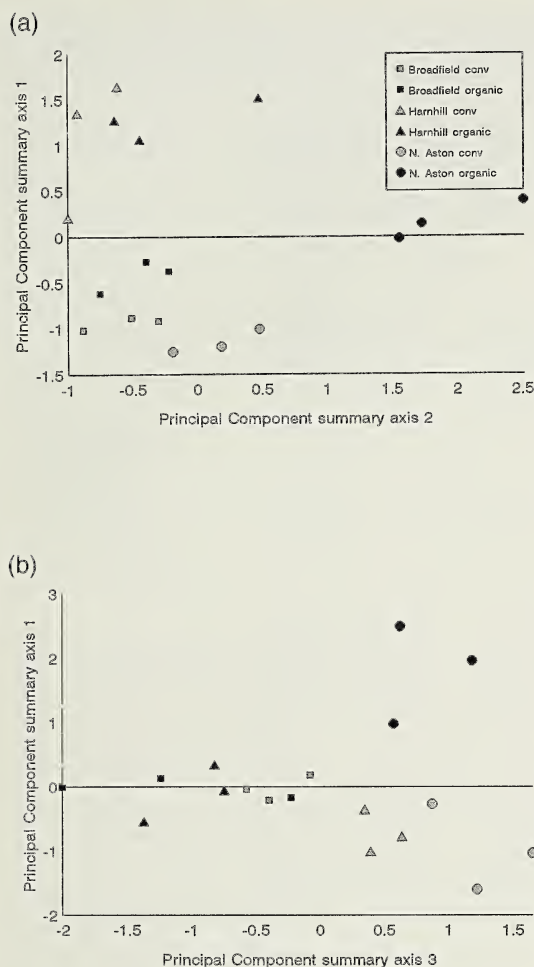
(a)

(b)

Figure 3.—Biplot showing location of organic and conventional fields with respect to first and second components derived from Principal Components Analysis applied to May sample (top graph), and first and third components derived from Principal Components Analysis applied to June sample (bottom graph).

samples from conventional fields. In this month, the species with highest loadings on the first axis were *E. atra*, *E. dentipalpis*, *Milleriana inerrans* (O.P.-Cambridge 1885) (Linyphiidae), *O. fuscus* and *Oedothorax retusus* (Westring 1851) (Linyphiidae) (0.59, 0.82, 0.95 and 0.78, respectively). Two species scored highly on the third: *M. rurestris* and *B. gracilis* (minus 0.67 and 0.87).

Relationship between vegetation data, spider abundance and spider species richness.—A number of vegetation variables differed significantly between organic and con-

ventional systems (Table 3). In both rounds, understory vegetation (both dicotyledonous and monocotyledonous species) was substantially more abundant on organic fields at two out of the three sites. Conventional fields had a higher crop density than organic fields. Crop height tended to be higher on organic than on conventional fields, although the North Aston site did not show this effect. There were no consistent patterns for the percentage cover of leaf litter and bare ground in either system.

In both months, there were significant positive relationships between the numbers of spiders caught and the percentage cover of dicotyledonous species and grasses within the crop. These relationships were significant both overall, and within each management system. Most other relationships were non-significant (Table 4), and the relationships with crop density can be explained as artifacts of the confounding effects of crop management.

In general, the patterns between the number of spider species caught and the vegetation data were similar to those for catch size. There was an inconsistent relationship between crop height and number of spider species caught, with a tendency for the relationship to be negative, particularly in the organic system (Table 5). As with catch size, the species richness of catches tended to be positively associated with the percentage cover of dicotyledonous and monocotyledonous species within the crop.

DISCUSSION

Arable ecosystems worldwide, whether high or low input, are characterized by a marked instability compared with natural communities. Their temporal and spatial structure militates against the persistence of populations of less mobile species, and major disruptions such as harvest (Topping & Sunderland 1994) and plowing (Haskins & Shaddy 1986) have negative effects on spider assemblages and are likely to exert the most over-riding effects. Our results showed, though, that contrasting arable farming systems can result in detectable differences in spider communities. Both the number of spiders captured and the species richness of spider samples were higher in organic than conventional winter wheat fields, significantly so at one site. Furthermore, our Principal Component Analyses suggested that spider communities as a whole differed between the con-

Table 3.—Mean values for vegetation variables on organic and conventional fields at each site in May and June (standard errors in parentheses). *** $P <$ 0.001, ** $P <$ 0.01, * $P <$ 0.05, ns not significant. See text for details of analysis.

Variable	Broadfield			Harnhill			North Aston		
	Conventional	Organic	Signif.	Conventional	Organic	Signif.	Conventional	Organic	Signif.
May									
crop density	101.4 (4.60)	42.4 (5.47)	***	105.0 (3.91)	79.1 (14.64)	*	127.4 (6.44)	106.3 (6.31)	ns
crop height	74.4 (1.14)	94.8 (0.95)	***	71.5 (3.48)	79.7 (2.21)	ns	87.4 (3.14)	78.2 (3.91)	*
% dicots	6.1 (2.16)	1.1 (0.32)	ns	3.8 (1.25)	18.1 (6.28)	*	0.14 (0.14)	11.2 (4.88)	*
% monocots	0.8 (0.83)	1.9 (0.77)	ns	1.25 (0.64)	5.7 (2.37)	ns	0.9 (0.50)	6.8 (2.64)	*
% leaf litter	1.4 (0.37)	2.6 (0.91)	ns	5.8 (2.50)	5.7 (2.07)	ns	14.3 (2.05)	6.7 (1.44)	**
% bare	63.2 (1.69)	90.8 (1.97)	***	67.5 (0.96)	55.5 (6.17)	ns	55.4 (3.56)	59.3 (6.42)	ns
June									
crop density	100.0 (1.61)	60.6 (3.64)	*	115.1 (6.25)	89.0 (20.28)	ns	139.3 (13.49)	106.5 (3.71)	*
crop height	82.6 (1.30)	113.6 (3.46)	ns	78.1 (3.54)	96.8 (1.28)	ns	94.3 (2.82)	92.3 (1.3)	ns
% dicots	1.3 (0.24)	0.4 (0.03)	ns	0.9 (0.40)	10.3 (1.94)	ns	0.6 (0.56)	9.1 (4.09)	ns
% monocots	1.4 (1.39)	0.6 (0.56)	ns	0.6 (0.29)	1.8 (0.89)	ns	1.1 (0.45)	5.4 (3.22)	*
% leaf litter	3.5 (1.21)	2.1 (0.83)	ns	10.1 (0.89)	12.5 (0.00)	ns	10.9 (2.07)	9.3 (0.77)	ns
% bare	74.9 (1.96)	88.6 (1.08)	**	62.9 (1.97)	60.9 (0.19)	ns	52.7 (4.17)	60.6 (4.18)	ns

Table 4.—The relationship between spider abundance and vegetation variables in May and June. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$. See text for details of analysis.

Variable	All sites		Organic		Conventional	
	r	P	r	P	r	P
May						
crop density	−0.26	***	−0.014	0.88	−0.055	0.57
crop height	−0.003	0.96	−0.087	0.373	−0.238	*
% dicots	0.279	***	0.147	0.127	0.201	*
% monocots	0.21	**	0.15	0.11	−0.001	0.99
% leaf litter	−0.303	***	−0.333	***	−0.142	0.142
% bare ground	−0.031	0.653	−0.191	*	−0.096	0.322
June						
crop density	−0.123	0.072	−0.003	0.969	0.028	0.774
crop height	−0.149	*	−0.400	***	−0.435	***
% dicots	0.255	***	0.221	*	0.222	*
% monocots	0.183	**	0.175	0.070	0.122	0.207
% leaf litter	−0.049	0.472	−0.081	0.403	−0.015	0.876
% bare ground	−0.147	*	−0.001	0.989	0.145	0.135

trasting management systems. While we could not interpret this difference in terms of the ecological characteristics of the species involved, these observations suggest that the habitat differences which are associated with these systems have a measurable impact on the spider communities.

Organic farming concentrates primarily on adjustments within the farm such as rotations and appropriate cultivations, rather than the use of inorganic fertilizers and pesticides, to achieve an acceptable level of output. It is ar-

gued that organic systems are more diverse, and therefore more stable, resulting in lower incidences of pest and disease problems, and increased biodiversity (Lampkin 1990). Many factors could thus contribute to our observed system effects. Our most consistent result was the increased abundance and species richness of spiders in our samples with increasing abundance of understory vegetation within the crop, both overall and within each system, within each sampling session. Web-building spiders are sensitive to changes in vegetation

Table 5.—The relationship between spider species richness and vegetation variables in May and June. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$. See text for details of analysis.

Variable	All sites		Organic		Conventional	
	r	P	r	P	r	P
May						
crop density	−0.21	**	−0.077	0.423	−0.093	0.337
crop height	−0.023	0.741	−0.065	0.501	−0.179	0.064
% dicots	0.174	*	0.067	0.487	0.066	0.497
% monocots	0.058	0.394	−0.014	0.882	−0.066	0.499
% leaf litter	−0.19	**	−0.21	*	−0.09	0.310
% bare ground	0.062	0.364	−0.031	0.749	0.025	0.794
June						
crop density	−0.107	0.117	0.009	0.921	0.118	0.222
crop height	−0.092	0.176	−0.376	***	−0.396	***
% dicots	0.245	***	0.196	*	0.177	0.067
% monocots	0.199	*	0.149	ns	0.166	0.087
% leaf litter	−0.028	0.678	−0.052	0.594	0.001	0.991
% bare ground	0.115	0.090	0.016	0.872	0.029	0.767

density (Topping 1993), biomass (Rypstra & Carter 1995), structure (Asteraki et al. 1992; Alderweireldt 1994) and height (Smith et al. 1993). The linyphiine spiders, most notably *B. gracilis* and *L. tenuis*, always anchor their sheet webs to the surrounding vegetation and never on bare soil alone, unlike *M. rurestris* and *Erigone* spp. which use small depressions in the soil (Alderweireldt 1994). Understory vegetation may assume increasing importance as senescence occurs in the lower leaves of the wheat stems (Sunderland et al. 1986) which is known to reduce overall spider abundance (Rypstra & Carter 1995). However, organic fields are not always weedier than conventional fields. Of our three sites, for example, one showed significantly lower abundances of understory vegetation on the organic compared to the conventional fields. This often occurs when a cereal crop follows a ryegrass/clover sward in the organic rotation.

Apart from the benefit of increased plant structure to web spinners, the growth of understory vegetation may offer polyphagous pests alternative food sources, and therefore benefit spiders indirectly (Rypstra & Carter 1995). Increased parasitism or predation of herbivorous pests may be partially responsible for a reduction of pest damage in weedy systems (e.g., Pavuk & Stinner 1992). Thus, a more complex community of predators, which includes spiders, could exert a significant controlling effect on prey species within the crop. We also recorded high numbers of spiders within our conventional fields, which may have been due to a temporary increase in spider abundance in response to high aphid densities.

Our data did not allow us to investigate the effects of agrochemical applications on the spider assemblages. Since spraying densities on conventional fields on the same farm were similar, and organic fields by definition had zero applications, agrochemical effects were entirely confounded with management system. However, various researchers have reported the declining abundance of predators with increased use of agrochemicals. In the Boxworth project, for example, the densities of Linyphiidae in areas receiving full pesticide inputs were approximately 47% those of levels in reduced-input areas (Grieg-Smith et al. 1991). Similar patterns were observed for

Staphylinidae and Coccinelidae (Coleoptera) (Vickerman 1991). In a study of twenty years of monitoring cereal fields in Sussex, Aebischer (1991) reported an overall annual decline rate of spiders of 4.1%, which effectively halved spider abundance over the study period, and agricultural intensification was cited as one likely explanation. Spiders in organic systems, while perhaps being subject to some aspects of intensification, such as spray drift from neighbouring land or poor water quality, should not suffer from major direct effects of pesticide use.

The spatial scale of land management changes is such that detecting significant effects of systems at the field scale can be very difficult. In the case of spiders which disperse by ballooning, which make up the greatest proportion of those inhabiting arable systems, the dominant landscape management is likely to exert the greatest influences on spider communities in an area. An organic farm is not isolated from these effects. That we were able to detect some differences in spider assemblages between the two systems, even under these circumstances, does suggest that the introduction of organic systems over wider areas may increase spider abundances disproportionately. However, a number of management strategies which are essential to organic farming can also be applied to conventional systems. Further studies are needed to understand whether effects similar to those of organic systems on arable species assemblages can be achieved under conventional systems if the management of the latter is modified appropriately.

LITERATURE CITED

Aebischer, N.J. 1991. Twenty years of monitoring invertebrates and weeds in cereal fields in Sussex. Pp. 305–332, *In* The Ecology of Temperate Cereal Fields. (L.G. Firbank, N. Carter, J.F. Dar-

byshire & G.R. Potts, eds.), Blackwell Scientific, Oxford. 469 pp.

Agnew, C.W. & J.W. Smith. 1989. Ecology of spiders (Araneae) in a peanut agroecosystem. Environ. Entomol., 18:30–42.

Alderweireldt, M. 1994. Prey selection and prey capture strategies of linyphiid spiders in high-input agricultural fields. Bull. British Arachnol. Soc., 9:300–308.

Asteraki, E.J., C.B. Hanks & R.O. Clements. 1992. The impact of the chemical removal of the hedge-base flora on the community structure of carabid beetles (Col., Carabidae) and spiders (Araneae) of the field and hedge bottom. J. Appl. Entomol., 113:398–406.

Barr, C.J., R.G.H. Bunce, R.T. Clarke, R.M. Fuller, M.T. Furse, M.K. Gillespie, G.B. Groom, C.J. Hallam, M. Hornung, D.C. Howard & M.J. Ness. 1993. Countryside Survey 1990, Main Report. Department of the Environment, London.

Bishop, L. 1990. Meteorological aspects of spider ballooning. Environ. Entomol., 19:1318–1387.

Bishop, L. & S.E. Riechert. 1990. Spider colonization of agroecosystems: mode and source. Environ. Entomol., 19:1738–1745.

Clausen, I.H.S. 1990. Design of research work based on a pilot study dealing with the effects of pesticides on spiders in a sugar-beet field. Acta Zool. Fennica, 190:75–87.

DeClercq, R. & R. Pietraszko. 1983. Epigeal arthropods in relation to predation of cereal aphids. Pp. 88–92, In Aphid Antagonists. (R. Cavalloro, ed.). A.A. Balkema, Rotterdam.

De Keer, R. & J. Maelfait. 1988. Observations on the life cycle of Erigone atra (Araneae, Erigoninae) in a heavily grazed pasture. Pedobiologia, 32:201–212.

El Titi, A. 1991. The Lautenbach Project, 1978–89. Pp. 399–411, In The Ecology of Temperate Cereal Fields. (L.G. Firbank, N. Carter, J.F. Darbyshire & G.R. Potts, eds.), Blackwell Scientific, Oxford.

Firbank, L.G., M.G. Telfer, B.C. Eversham & H.R. Arnold. 1994. The use of species decline statistics to help target conservation policy for set-aside arable land. J. Environ. Manage., 42:415–422.

Fuller, R.M. 1987. The changing extent and conservation interest in lowland grasslands in England and Wales: a review of the grassland surveys 1930–84. Biol. Conserv., 40:281–300.

Gibbons, D.W., J.B. Reid & R.A. Chapman. 1993. The New Atlas of Breeding Birds in Britain and Ireland: 1988–1991. A.D. Poyser, London.

Gluck, E. & S. Ingrish. 1990. The effect of biodynamic and conventional agriculture management on Erigoninae and Lycosidae spiders. J. Appl. Entomol., 110:136–148.

Greig-Smith, P.W., G.K. Frampton & A.R. Hardy.

1991. Pesticides, Cereal Farming and the Environment: The Boxworth Project. HMSO, London.

Harvey, P.H. & M.D. Pagel. 1991. The Comparative Method in Evolutionary Biology. Oxford Univ. Press, Oxford.

Haskins, M.F & J.H. Shaddy. 1986. The ecological effects of burning, mowing and plowing on ground-inhabiting spiders (Araneae) in an old-field system. J. Arachnol., 14:1–13.

Jordan, V.W.L. & J.A. Hutcheon. 1995. Less intensive farming and the environment: an Integrated Farming Systems approach for UK arable crop rotation. Pp. 307–318, In Ecology and Integrated Farming Systems. (D.M. Glen, M.P. Greaves & H.M. Anderson, eds.). Wiley, Chichester.

Lampkin, N. 1990. Organic Farming. Farming Press Books, Ipswich, 701 pp.

Luff, M.L. & M.D. Eyre. 1988. Soil-surface activity of weevils (Col: Curculionoidea) in grassland. Pedobiologia, 32:39–46.

Mangan, R.L. & R.A. Byers. 1989. Effect of minimum tillage on spiders. Environ. Entomol., 18: 945–952.

McKone, M.J. & C.M. Lively. 1993. Statistical analysis of experiments conducted at multiple sites. Oikos, 67:184–186.

Merrett, P. & R. Snazell. 1983. A comparison of pitfall trapping and vacuum sampling for assessing spider faunas on heathland at Ashdown Forest, south-east England. Bull. British Arachnol. Soc., 6:1–13.

Moore, N.W. 1962. The heaths of Dorset and their conservation. J. Ecol., 50:369–391.

Newton, I. & I. Wyllie. 1992. Recovery of a sparrowhawk population in relation to declining pesticide contamination. J. Appl. Ecol., 29:476–484.

Nyffeler, M. & G. Benz. 1988. Spiders in natural pest control: a review. J. Appl.Entomol., 103: 321–339.

Pavuk, D.M. & B.R. Stinner. 1992. Influence of weed communities in corn planting on parasitism of Ostrina nubilalis (Lepidoptera: Pyralidae) by Eriborus terebrans (Hymenoptera: Ichneumonidae). Biol. Control, 2:312–316.

Pielou, E.C. 1984. The Interpretation of Ecological Data: A Primer on Classification and Ordination. Wiley-Interscience, New York.

Potts, G.R. 1991. The environmental and ecological importance of cereal fields. Pp. 3–23, In The Ecology of Temperate Cereal Fields. (L.G. Firbank, N. Carter, J.F. Darbyshire & G.R. Potts, eds.). Blackwell Scientific, Oxford. 469 pp.

Potts, G.R. & N.J. Aebischer. 1991. Modelling the population dynamics of the grey partridge: conservation and management. Pp. 373–390, In Bird Population Studies: Their Relevance to Management. (C.M. Perrins, J.-D. LeBreton & G.J.M. Hirons, eds.). Oxford University Press.

Riechert, S.E. & T. Lockley. 1984. Spiders as bi-
ological control agents. Ann. Rev. Entomol., 29:
299–320.

Roberts, M.J. 1987. The Spiders of Great Britain
and Ireland. Volume 2: The Linyphiidae. Harley
Books, Colchester.

Rypstra, A.L. & P.E. Carter. 1995. The web-spider
community of soybean agroecosystems in south-
western Ohio. J. Arachnol., 23:135–144.

SAS Institute Inc. 1988. SAS/STAT User's Guide.
Release 6.03 Edition. SAS Institute Inc., Cary,
North Carolina.

Smith, H., R.E. Feber, P.J. Johnson, K. McCallum,
S. Plesner Jensen, M. Younes & D.W. Macdon-
ald. 1993. The Conservation Management of
Arable Field Margins. English Nat. Sci., No. 18.
English Nature, Peterborough.

Stewart, A., D.A. Pearman, D.A. & C.D. Preston.
1994. Scarce Plants in Britain. Peterborough.

Sunderland, K.D., A.M. Fraser & A.F.G. Dixon.
1986. Field and laboratory studies on money spi-
ders (Linyphiidae) as predators of cereal crops.
J. Appl. Ecol., 23:433–447.

Topping, C.J. 1993. Behavioural responses of three

linyphiid spiders to pitfall traps. Entomol. Exp.
Appl., 68:287–293.

Topping, C.J. & K.D. Sunderland. 1992. Limita-
tions to the use of pitfall traps in ecological stud-
ies exemplified by a study of spiders in a field
of winter wheat. J. Appl. Ecol., 29:485–491.

Topping, C.J. & K.D. Sunderland. 1994. Methods
for quantifying spider density and migration in
cereal crops. Bull. British Arachnol. Soc., 9:209–
213.

Vickerman, G.P. 1991. The effects of different pes-
ticide regimes on the invertebrate fauna of winter
wheat. Pp. 82–109, In The Boxworth Project:
Pesticides, Cereal Farming and the Environment
(P.W. Greig-Smith, G.K. Frampton & A.R. Har-
dy, eds.). HMSO, London.

Webb, N.R. 1990. Changes on the heathlands of
Dorset, England between 1978 and 1987. Biol.
Conserv., 51:273–286.

Young, O.P & G.B. Edwards. 1990. Spiders in
United States field crops and their potential effect
on crop pests. J. Arachnol., 18:1–27.

HABITAT STRUCTURE AND PREY AVAILABILITY AS PREDICTORS OF THE ABUNDANCE AND COMMUNITY ORGANIZATION OF SPIDERS IN WESTERN OREGON FOREST CANOPIES

Juraj Halaj[1,3], Darrell W. Ross[2] and Andrew R. Moldenke[1]: [1]Department of Entomology, Oregon State University, Corvallis, Oregon 97331 USA; and [2]Department of Forest Science, Oregon State University, Corvallis, Oregon 97331 USA.

ABSTRACT. The significance of habitat structure and prey availability in spider biology has been well investigated in a number of communities, but only briefly in forest canopies. This study gathered indirect evidence for the importance of these two factors as determinants of spider abundance and diversity in arboreal communities of western Oregon. Arthropods were collected by harvesting and bagging tips (1 m long) of lower crown branches from red alder (*Alnus rubra*), western redcedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), noble fir (*Abies procera*) and Douglas-fir (*Pseudotsuga menziesii*). Several characteristics of arthropod habitats were measured: tree diameter at breast height, maximum horizontal and vertical branch spread, number of branching angles and leaves, and total biomass of twigs and foliage. The highest numbers of spiders per branch were collected from structurally more complex tree species including Douglas-fir and noble fir. These tree species also had the highest spider species richness. The greatest similarity in spider community structure was found among tree species with shared branch characteristics such as needles. The biomass of foliage and prey availability were the best predictors of spider abundance on individual tree species. Biomass of twigs alone accounted for almost 70% and 60% of the variation in total spider abundance and species richness, respectively, across a wide range of arboreal habitats. Prey availability accounted for less of the variation. Selected habitat variables also predicted the abundance of several prey groups including Aphidoidea, Psocoptera, Diptera and Collembola. Our results suggest that habitat structure and prey availability in combination may play significant roles in structuring the spider community of western Oregon forest canopies.

The significance of habitat structure in spider biology has been a topic of numerous ecological studies. This interest is undoubtedly due to the great abundance and diversity of spiders (Coddington & Levi 1991), the variety of ecological roles they play (Foelix 1982; Wise 1993) and the intimate dependence of these arachnids on specific habitat features ensuring an optimal thermal environment, proper construction of their webs and retreats, and conduction of vibratory signals (Foelix 1982; Riechert & Gillespie 1986; Uetz 1991). The importance of habitat structure relative to the abundance and community structure of spiders has been extensively studied in a variety of natural communities including deserts (Riechert 1976; Lubin et al. 1993), grasslands and

shrub communities (Duffey 1978; Schaefer 1978; Hatley & MacMahon 1980), and forest floor (Uetz 1975; Cady 1984; McIver et al. 1992).

Trees are architecturally diverse habitats supporting a remarkable array of arthropods (Strong et al. 1984). Spiders are an important component of these arboreal arthropod communities in temperate (Moldenke et al. 1987; Schowalter 1995; Halaj et al. 1996, 1997) and tropical forests (Stork 1991; Russell-Smith & Stork 1994). Their predatory role in some canopy systems has been well documented (Loughton et al. 1963; Fichter 1984). Despite the apparent dependence of spiders on habitat structure and their implied importance in forest canopies, relatively few studies have investigated spider-habitat interactions in these systems. Stratton et al. (1979) investigated spider assemblages associated with branches of red pine (*Pinus resinosa*), white spruce

[3]Correspondence and present address: Department of Zoology, Miami University, Oxford, Ohio 45056 USA.

(*Picea glauca*), and white cedar (*Thuja occidentalis*) in northeastern Minnesota. Tree species differed significantly in spider abundance and community structure, probably due mostly to differences among the tree species in the branch physical structure. Jennings & Dimond (1988) and Jennings et al. (1990) suggested that curved needles of red spruce (*Picea rubens*) provide a better habitat for spiders than flat needles of balsam fir (*Abies balsamea*) in east-central Maine. In a series of studies conducted in southern Sweden (Gunnarsson 1988; 1990; Sundberg & Gunnarsson 1994), it has been suggested that a higher needle density of Norway spruce (*Picea abies*) improves spider habitat quality, possibly by providing increased protection against foliage-foraging birds (Askenmo et al. 1977).

The objective of this study was to make initial observations of how habitat structure and prey availability influence arboreal spiders in western Oregon. We intended to determine if there were significant associations between selected habitat variables of several host-tree species and the abundance and diversity of associated arthropod fauna. By investigating several host-tree species with fundamentally different branch structure simultaneously, we could identify commonalities of spider habitats across a wide range of arboreal communities. Based on indirect observational evidence and experimental data from some arboreal systems (e.g., Stratton et al. 1979; Gunnarsson 1990), we hypothesized that spider abundance and community structure could be predicted by a combination of the availability and characteristics of their habitats, and prey abundance in tree canopies.

METHODS

Study sites and tree species.—This study was conducted at the H.J. Andrews Experimental Forest (44°13'30"N, 122°09'46"W), a Long-Term Ecological Research Site, and UNESCO Man and the Biosphere Reserve, in the western Cascade Range of Oregon, near Blue River, in Lane and Linn Counties, USA. Six study sites were selected in March 1993. The main criterion for site selection was the presence of at least 20 dominant or co-dominant trees (diameter at breast height < 20cm) of the selected species at a particular site. Tree species chosen included: red alder (*Alnus rubra*), western redcedar, (*Thuja plicata*), west-

ern hemlock, (*Tsuga heterophylla*), noble fir (*Abies procera*) and Douglas-fir (*Pseudotsuga menziesii*) (Table 1). These are common species found in western Oregon (Franklin & Dyrness 1988), and they possess a broad range of structural characteristics.

Lower elevation sites: Three study sites identified as A, B and C were selected at elevations ranging from 597–805 m in the *Tsuga heterophylla* zone (Franklin & Dyrness 1988). This is a temperate, mesophytic formation with a wet and mild maritime climate. The mean annual precipitation and temperature range from 1500–3000 mm, and 7.4–10.4 °C, respectively (Franklin & Dyrness 1988). Tree species sampled on each of the sites in this zone included red alder, western redcedar, western hemlock, and Douglas-fir. The ground vegetation was dominated by Pacific rhododendron (*Rhododendron macrophyllum), Berberis nervosa* and bracken fern (*Pteridium aquilinum*).

Higher elevation sites: Since noble fir occurs at lower elevations only sparsely, three additional study sites (D, E and F) were added to sample this tree species at elevations ranging from 1195–1292 m in the *Abies amabilis* zone (Franklin & Dyrness 1988). This zone is considered a cool or subalpine formation with a short growing season and significant snowfall. The mean annual precipitation and temperature range from 2100–3000 mm, and 5.5–6.0 °C, respectively (Franklin & Dyrness 1988). The study site vegetation included dense patches of beargrass (*Xerophylum tenax*), salal (*Gaultheria shallon*) and various berries (*Vaccinium* spp.). As a reference, co-occurring Douglas-fir was also sampled at these higher elevation sites. At all sites, trees were selected along a transect (10 m × 50 m) placed in the forest stand. This procedure was repeated by selecting multiple transects until 20 trees of each species occurring at the particular site were designated. Thus, the size of the study site was determined by the number and distribution of sampled trees. With the exception of occasional pockets of red alder and western redcedar, this procedure normally resulted in sampling fairly interspersed trees of all species.

Field and laboratory procedures.—On each tree, four accessible non-interdigitated tips of branches (sampling units) of constant length (1 m) were removed arbitrarily from

Table 1.—Summary of study site and tree characteristics potentially important to arthropod habitat quality. Statistics are results of two-way ANOVAs to compare habitat variables separately at lower and higher study sites. Means (± SE) followed by different letters are significantly different (LSD; $P < 0.01$). * Indicates a significant site by host-tree species interaction effect.

Host species	Elev. range (m)	Sampling period	Trees sampled (n)	Diameter at breast height (cm)	Horiz. branch spread (cm)	Vertic. branch spread (cm)	Foliage biomass (g)	No. leaves (n)	Wood biomass (g)	No. branching angles (n)
Lower sites										
Red alder	597–805	June 13–26	57	4.27 (0.28)b	39.17 (1.48)d	25.10 (0.84)d	19.91 (0.77)d	126.57 (4.50)b	24.83 (0.88)d	28.46 (1.50)b
Western redcedar		June 10–28	60	13.90 (0.77)a	69.11 (1.35)b	39.81 (1.08)a	110.65 (3.82)a	278.62 (6.04)a	48.42 (1.56)c	16.15 (0.29)c
Western hemlock		June 12–29	60	14.41 (0.73)a	63.28 (1.26)c	28.42 (0.65)c	78.17 (3.30)c	—	54.12 (1.88)b	—
Douglas-fir		June 2–July 2	60	14.31 (0.66)a	76.51 (1.56)a	32.04 (1.02)b	95.83 (3.49)b	—	65.68 (2.20)a	120.91 (5.65)a
				$F = 75.37$* $df = 3,225$ $P < 0.001$	$F = 146.86$ $df = 3,224$ $P < 0.001$	$F = 48.16$* $df = 3,224$ $P < 0.001$	$F = 488.87$* $df = 3,225$ $P < 0.001$	$F = 435.45$* $df = 1,111$ $P < 0.001$	$F = 175.41$* $df = 3,225$ $P < 0.001$	$F = 729.39$* $df = 2,168$ $P < 0.001$
Higher sites										
Noble fir	1195–1292	July 3–11	60	13.67 (0.43)	69.21 (1.28)	15.61 (0.51)b	195.79 (5.63)a	—	118.28 (3.15)a	235.07 (8.07)a
Douglas-fir		July 4–12	60	14.40 (0.50)	67.72 (1.09)	29.77 (0.69)a	132.95 (4.02)b	—	89.15 (2.46)b	129.32 (4.78)b
				$F = 0.13$ $df = 1,114$ $P = 0.719$	$F = 0.58$ $df = 1,114$ $P = 0.447$	$F = 361.80$* $df = 1,114$ $P < 0.001$	$F = 89.32$ $df = 1,114$ $P < 0.001$		$F = 56.44$ $df = 1,114$ $P < 0.001$	$F = 159.83$* $df = 1,114$ $P < 0.001$

the lower third of the tree canopy with a hand pruner. Each branch was quickly placed in a heavy-duty plastic bag and transported to the laboratory. In order to prevent cannibalism in sample bags, and to facilitate the removal of arthropods from the branches, a 3 sec spray of a pyrethrin-based insecticide (Hi-Power™ Ant, Roach & Spider Spray Formula II; Ortho, San Ramon, California, USA) was applied inside each bag before sealing it. In the laboratory, each sample branch was shaken vigorously within the bag to remove arthropods. Dislodged arthropods were collected by washing the bag with tap water. All specimens were preserved in 75% ethyl alcohol.

Spiders were sorted and identified to the lowest possible taxa, and further categorized into eight functional groups based on foraging strategy similarities. Hunting spiders included: (1) agile hunters of the families Salticidae and Oxyopidae, (2) ambushers of the family Thomisidae, (3) runners of the family Philodromidae and (4) nocturnal hunters comprising Clubionidae, Anyphaenidae and Gnaphosidae. Web builders were divided into categories of spiders with similar web characteristics and included: (1) orb weavers of the families Araneidae, Tetragnathidae, and Uloboridae, (2) cobweb spiders, family Theridiidae, (3) sheet-web weavers of the family Linyphiidae and (4) hackled-band weavers, family Dictynidae. The rest of the arthropod community was sorted and identified to order. The abundance of all arthropods other than spiders was used as an estimate of the spider food base. Voucher specimens of arthropods collected in this study have been deposited in the insect collection of the Systematic Entomology Laboratory, Department of Entomology, Oregon State University, Corvallis, Oregon, USA.

To obtain a manageable group of branches, three out of four branches harvested from each tree were randomly selected to measure several characteristics of spider habitat. To assess arthropod-habitat relationships, only the arthropods collected from this subset of branches were used in correlation analyses; but arthropod abundance and diversity, however, were compared using specimens from all four branches. Maximum horizontal and vertical branch spread (cm) were defined as maximum perpendicular distances to the branch axis, measured horizontally and vertically, re-

spectively. We hypothesized that increased spread of branches would increase the probability of intercepting spiders during their dispersal by ballooning, and thus may be a reliable indicator of their abundance in the canopy. Conversely, flatter branches with shorter vertical spread might increase the exposure of spiders to visually foraging predators (e.g., birds) and thus be negatively correlated with spider densities. Total number (n) of branching angles (axils) was defined as the number of acute angles, measured between two branchlets. The number of branching angles reflects the architectural complexity of the branch, and thus may be related to the quality of the spider habitat. The number of leaves (n) was counted on alder branches, whereas composite leaves were counted on branches of western redcedar. Total biomass of foliage and stems (g) was estimated separately by weighing after oven-drying. These variables are correlated with the total amount of available surface area on the branch, and may also reflect its structural complexity. Diameter (cm) at breast height (1.3 m above ground) was measured on each tree. Tree diameter is directly related to tree size, and may provide an indirect measure of the total amount of spider habitat available on a particular tree.

Statistical analyses.—The number and diversity of arthropods, and values of habitat variables measured on individual branches were averaged for each tree (experimental unit). This estimate was used in all statistical analyses. Differences in arthropod abundance on individual tree species were assessed with multi-factor ANOVA, with tree species and sites as factors. All treatment means were compared and separated with the Fisher's protected least significant difference (LSD) test (Steel & Torrie 1980). Lower and higher elevations were compared with a t-test. In order to satisfy the assumption of homogeneous variance in ANOVA, variables were ln-transformed, as appropriate, prior to all analyses. In all cases, the original means and their standard errors are reported here. Spider diversity was estimated with the Shannon diversity index (H') (Pielou 1975). Overlap in the spider community structure and species composition were estimated with the formula in Schoener (1968) and with the Sørensen similarity index (C_s) (Southwood 1992), respectively. Multiple

regression analyses were used to select the best subset of habitat variables predicting arthropod abundance and spider diversity: (1) individually for each host-tree species (using samples pooled across all sites at which it occurred) and (2) across host-tree species (using samples pooled from all tree species and sites). Since we expected predictor variables to be linearly related, stepwise procedures were used to control for multicolinearity among the variables. Adjusted R^2 values were used to select best regression models; maximum R^2 and minimum mean square error terms were used as variable selection criteria. All statistical analyses were performed with SAS computer programs (SAS Institute Inc. 1994).

RESULTS

Arthropod habitat characteristics.— There were significant differences in branch characteristics among host-tree species (Table 1). With the exception of red alder, all tree species across lower elevation sites were similar in size as measured by their trunk diameter. In addition, Douglas-fir trees of similar size were sampled at lower and higher elevations ($t = 0.05$; $df = 4$; $P = 0.962$). At lower elevations, branches of Douglas-fir had the widest horizontal spread, the highest number of branching angles, and contained the greatest amount of wood biomass. Branches of redcedar had the greatest vertical spread, reflecting the "hanging" arrangement of its foliage, and provided the greatest amount of foliage biomass per 1 m branch tip (Table 1). There were no differences in the horizontal spread of Douglas-fir and noble fir branches across higher elevation sites. Branches of noble fir were significantly flatter, but contained significantly more branch biomass and number of branching angles than those of Douglas-fir. Douglas-fir at higher elevations had narrower branches, but contained significantly more branch biomass (all $P < 0.05$) than individuals of the same species at lower sites (Table 1).

Spider abundance.— There were significant differences in the total numbers of spiders per branch tip among host-tree species across lower elevation sites ($F = 108.23$; $df = 3,225$; $P < 0.001$; Fig. 1A). Although spider densities varied with sites ($F = 4.44$; $df = 2,225$; $P = 0.013$), host-tree effects were

site independent (species*site interaction; $F = 1.03$; $df = 6,225$; $P = 0.406$). The highest spider densities at lower elevations were collected from Douglas-fir (mean ± SE; 5.36 ± 0.54), whereas red alder supported the lowest densities per branch tip (0.85 ± 0.14). Spider densities on hemlock (2.63 ± 0.22) and redcedar (2.06 ± 0.13) were not significantly different, and were intermediate compared with red alder and Douglas-fir. Significantly more spiders were collected from Douglas-fir branches (9.92 ± 0.47) compared with noble fir (8.20 ± 0.33) at higher elevations ($F = 6.46$; $df = 1,114$; $P = 0.012$), and similar differences between these two species were present at all higher sites (Fig. 1A). In addition, significantly more spiders were found at higher than lower-site Douglas-fir ($t = 6.69$; $df = 4$; $P = 0.003$).

Among hunting spiders, densities of agile and nocturnal hunters followed a similar trend as overall spiders across tree species, with the lowest numbers on red alder and the highest numbers on Douglas-fir ($F = 34.08$; $df = 3,225$; $P < 0.001$, and $F = 11.02$; $df = 3,225$; $P < 0.001$, respectively; Fig. 2A, B). Densities of both spider groups on Douglas-fir and noble fir, however, were not statistically different. All trends for these two spider groups were similar across sites (all species*site terms; $P > 0.05$). Densities of running spiders tended to be significantly higher on redcedar, and on Douglas-fir at lower elevations ($F = 14.91$; $df = 3,225$; $P < 0.001$), and with the exception of site D, greater on Douglas-fir than noble fir at higher elevations ($F = 26.16$; $df = 1,114$; $P < 0.001$; Fig. 2C). Both trends for running spiders, however, were slightly inconsistent as indicated by significant species*site interactions ($P = 0.04$, and $P = 0.015$, respectively). Douglas-fir at both elevation ranges supported a similar abundance of agile hunters ($t = 1.84$, $df = 4$; $P = 0.140$); however, there were more running spiders and nocturnal hunters collected from higher than lower-site Douglas-fir ($P = 0.006$, and $P = 0.005$, respectively).

Densities of sheet-web weavers varied significantly among the tree species, being highest on Douglas-fir, followed by hemlock, redcedar and red alder ($F = 84.57$, $df = 3,225$; $P < 0.001$; Fig. 3A). This tree species effect, however, was site-dependent ($F = 5.93$; $df = 6,225$; $P < 0.001$). For example, there were
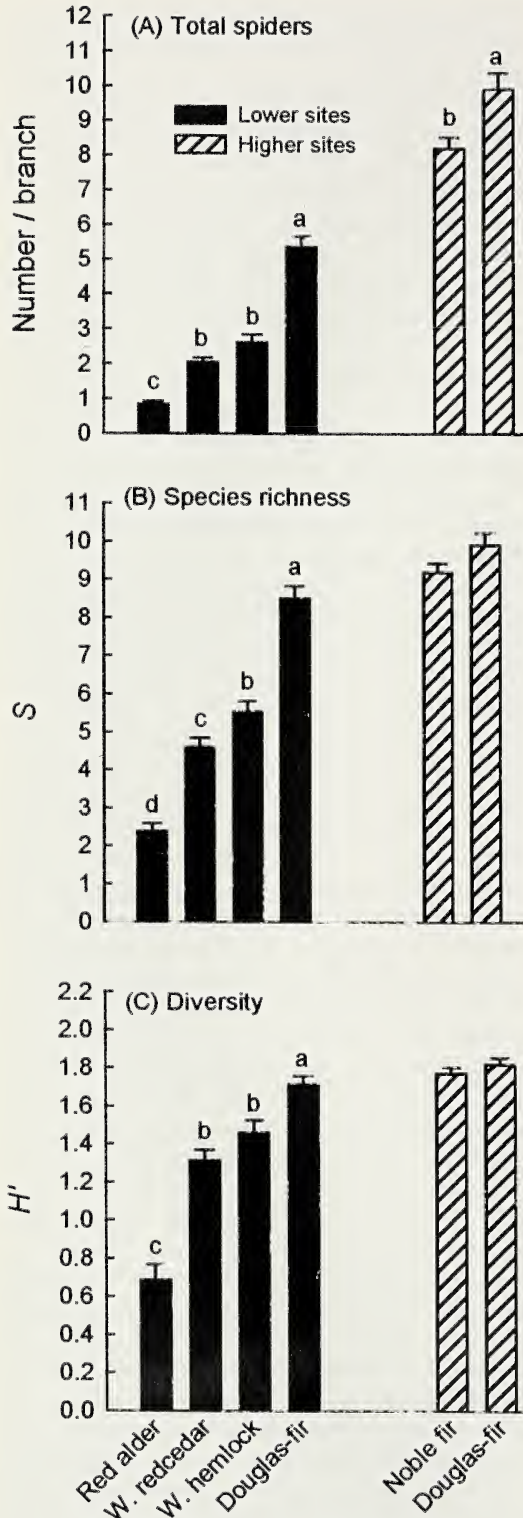
no differences between hemlock and Douglas-fir at site C, or alder and redcedar at site A. Both Douglas-fir and noble fir supported equal densities of these spiders at higher elevations (Fig. 3A). There were more sheet-web weavers collected from Douglas-fir at higher than at lower sites; the trend, however, was not statistically significant ($t = 1.54$; $df = 4$; $P = 0.197$). Significantly more orb-weavers were collected from redcedar and Douglas-fir than red alder and hemlock at all lower sites (F = 5.93, $df = 3,225$; $P < 0.001$), and from Douglas-fir than noble fir at all higher sites ($F = 20.48$, $df = 1,114$; $P < 0.001$; Fig. 3B). In addition, there was a significant positive effect of elevation for orb-weavers on Douglas-fir ($t = 3.40$, $df = 4$; $P = 0.027$). Overall, densities of cobweb spiders tended to be significantly greater on Douglas-fir than any other tree species at lower elevations ($F = 18.46$, $df = 3,225$; $P < 0.001$; Fig. 3C). This trend, however, was site-dependent; for example, there were no differences among tree species at site A. Douglas-fir and noble fir supported approximately equal densities of cobweb spiders at all high elevation sites, and similarly there were no significant differences in cobweb spider abundance between lower and higher-elevation Douglas-fir (all $P > 0.05$).

Non-Araneae arthropod abundance.— The abundance of potential spider prey varied significantly with host-tree species ($F = 21.67$, $df = 3,219$; $P < 0.001$; Fig. 4A). Douglas-fir consistently supported the highest densities of potential prey individuals per branch tip (21.33 ± 3.23), followed by western hemlock (15.98 ± 2.80) and red alder (15.48 ± 1.79), whose prey densities did not differ significantly. Redcedar provided the lowest prey abundance among the tree species (9.14 ± 1.15). Similarly, Douglas-fir supported larger arthropod numbers than noble fir (36.41 ± 2.35, and 18.29 ± 1.39, respectively) at higher elevations ($F = 63.96$, $df = 1,114$; $P < 0.001$), and a significant species*site term ($F = 5.20$, $df = 2,114$; $P = 0.007$) reflected only a varying magnitude of

←

richness and diversity were calculated from all specimens collected on one tree (four branches per tree). Bars with different letters are statistically different (LSD; $P < 0.05$).
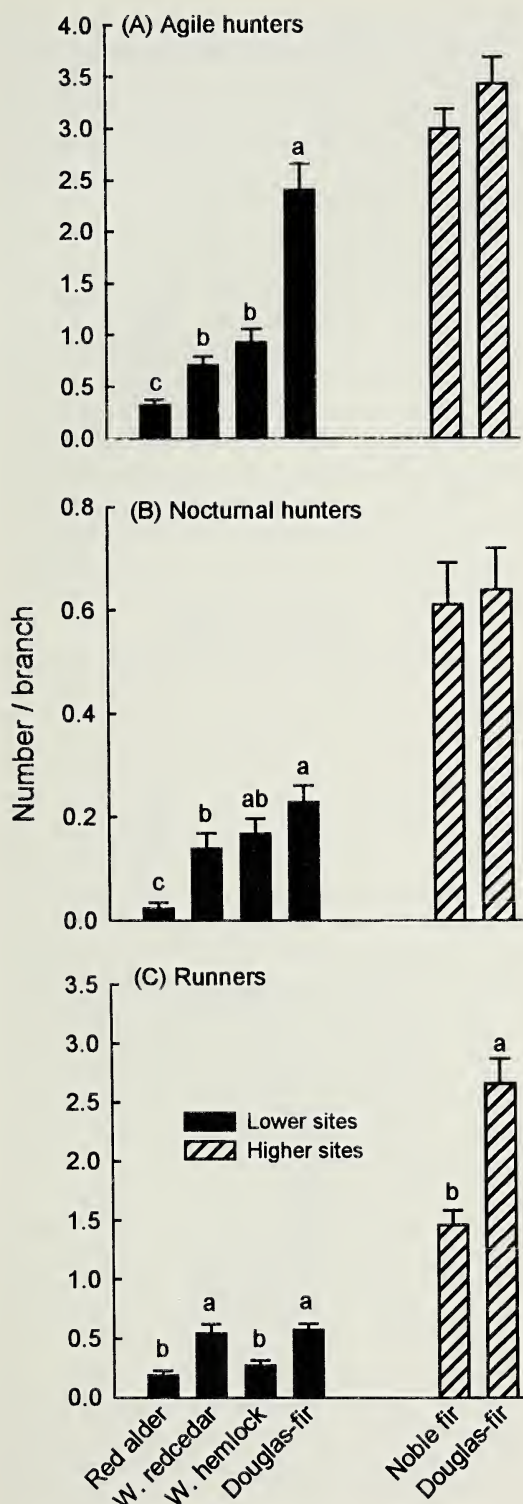
Figure 1.—Mean values ($\pm$ SE) of total spider density (A), species richness (B) and species diversity (C) on individual host-tree species. Species

Figure 2.—Mean densities (± SE) of agile hunters (A), nocturnal hunters (B) and runners (C) on individual host-tree species. Bars with different letters are statistically different (LSD; $P < 0.05$).

difference between these two species (Fig. 4A). Aphids, the most abundant potential prey species collected in the study (29.10% of all non-Araneae arthropods), were significantly more abundant on red alder and Douglas-fir than on redcedar and hemlock which supported similarly low densities ($F = 100.77$, $df = 3,219$; $P < 0.001$; Fig. 4B). Aphid densities were greater on Douglas-fir than noble fir at higher elevations ($F = 55.93$, $df = 1,114$; $P < 0.001$), however, the magnitude of the difference varied with sites ($F = 3.88$, $df = 2,114$; $P = 0.023$). Branches of Douglas-fir supported significantly more total non-Araneae arthropods and Aphidoidea at higher than lower elevations ($t = 4.98$; $df = 4$; $P = 0.008$, and $t = 3.86$; $df = 4$; $P = 0.018$, respectively). Psocoptera were the second most abundant potential prey organisms (14.0%). Their abundance was consistently greater on Douglas-fir, hemlock, and redcedar than red alder ($F = 146.90$, $df = 3,219$; $P < 0.001$), nevertheless, the magnitude of difference varied with sites (species*site: $P = 0.008$). Douglas-fir and noble fir had consistently similar densities of psocids at higher elevations (Fig. 4C). Although on average there were more psocids collected from lower than higher-site Douglas-fir, this trend was not statistically significant ($t = 1.58$; $df = 4$; $P = 0.189$).

Spider community structure.—There were significant differences in the number of spider species and their diversity among the tree species at lower elevations ($F = 97.50$, $df = 3,225$; $P < 0.001$, and $F = 54.72$, $df = 3,223$; $P < 0.001$, respectively; Fig. 1B,C). On average, the highest number of species was collected from Douglas-fir (8.50 ± 0.32), followed by western hemlock (5.52 ± 0.29), redcedar (4.60 ± 0.24), and red alder (2.37 ± 0.21). With the exception of site B (interaction term for richness: $F = 3.22$, $df = 6,225$; $P = 0.005$, and diversity $F = 2.30$, $df = 6,223$; $P = 0.04$), this trend was consistent across all lower elevation sites. A similar number of species and diversity were found on Douglas-fir (species; 9.90 ± 0.32) and noble fir (species; 9.18 ± 0.24) at all higher sites (Fig. 1B,C). There were no significant differences in spider species richness or diversity between lower and higher-elevation Douglas-fir ($P = 0.186$, and $P = 0.182$, respectively).

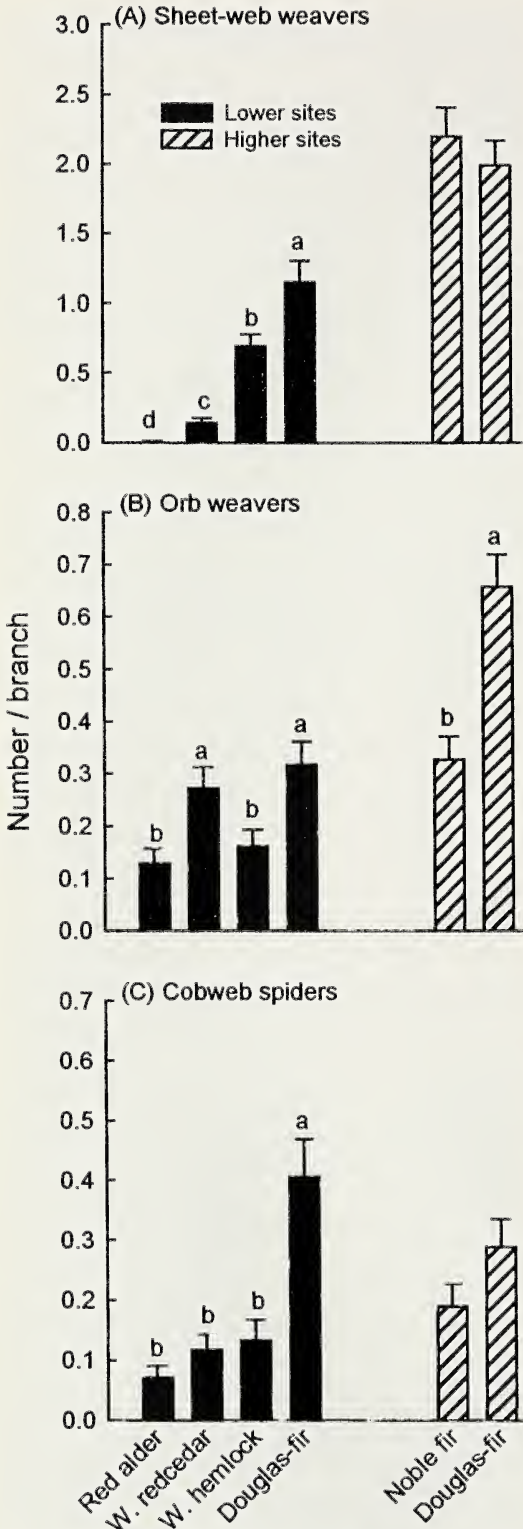Numerically, hunting spiders dominated the spider community on all host-tree species

Figure 3.—Mean densities (± SE) of sheet-web weavers (A), orb-weavers (B), and cobweb spiders (C) on individual host-tree species. Bars with different letters are statistically different (LSD; $P < 0.05$).

(Fig. 5). Agile hunters and runners were the dominant hunting groups, and a salticid, *Metaphidippus aeneolus* Curtis 1892, accounted for as much as 55% of hunting spiders and 35% of all spiders in the arboreal community (Fig. 5, Table 2). The guild of web-building spiders on red alder and redcedar was dominated by orb-weavers, whereas sheet-web weavers were predominant among web-building spiders on conifers with needles (Fig. 5). The highest similarities in the community structure were found between Douglas-fir and western hemlock at lower sites, with an overlap ranging from 83–94%, and Douglas-fir and noble fir at higher elevations (81–91%). Conifers with needles also shared as much as 74–80% of spider species (Table 3). Similarities in spider community structure and species composition between lower and higher-site Douglas-fir were ranging from 67–91%, and 71–81%, respectively.

Arthropod-habitat associations.—*Patterns on individual host-tree species:* Spider abundance was significantly associated with habitat variables of individual host-tree species (Table 4). From 10–45% of variation in spider abundance was associated with the amount of foliage and prey abundance on branch tips. In red alder, number of leaves and leaf biomass alone explained 13% and 16% of the variation, respectively; the contribution of prey abundance alone was 13%. On western hemlock, foliage biomass accounted for 36%, whereas prey abundance alone accounted for 19% of variation in spider abundance, respectively. Although abundance of prey alone was selected as the best predictor of spider abundance on noble fir, foliage biomass alone could explain 12% of the variation. As much as 22% of variation in spider abundance on Douglas-fir at lower elevations was assigned to foliage biomass, whereas the number of branching angles contributed 15%; vertical branch spread and tree diameter alone contributed only 5 and 0.4%, respectively.

Patterns across all host-tree species: As much as 75% of variation in the total abundance of spiders on sampled trees was related to the amount of foliage, wooden twigs, and prey availability (Table 5). The amount of wooden twigs alone accounted for 68% of the variation in spider abundance across a wide range of arboreal habitats on five tree species with great differences in their branch architec-
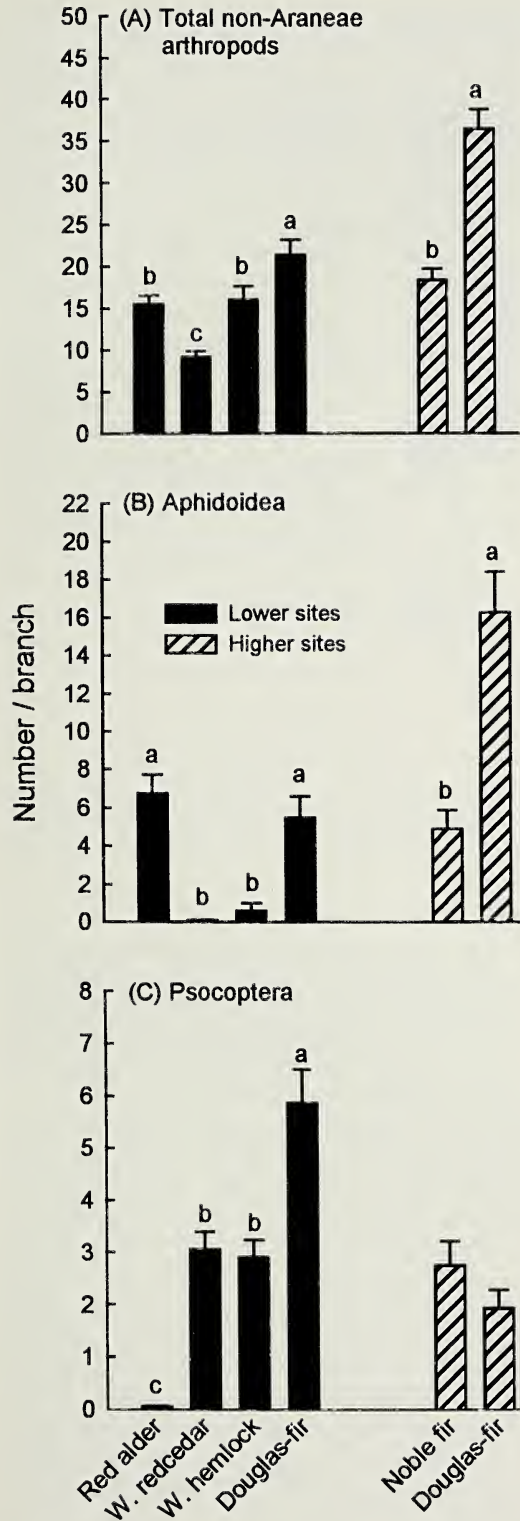
Figure 4.—Mean densities (± SE) of total potential spider prey organisms (A), aphids (B) and psocids (C) on individual host-tree species. Bars with different letters are statistically different (LSD; $P < 0.05$).

ture. The amount of foliage biomass explained almost 60% of the variation in spider abundance, and the availability of prey accounted for approximately ¼ of the variation. Adding these two variables into the prediction model, however, resulted in only a slight increase in its fit (7%) after accounting for the predictive power of wooden twigs (Table 5, Fig. 6). Biomass of wooden twigs alone was also a fair predictor of the abundance of agile hunters, sheet-web weavers and runners, explaining 49%, 44% and 34% of the variation in the abundance of these spider groups, respectively. The habitat variables measured in this study, however, did not appear to be strong predictors of the abundance of nocturnal hunters, or orb and cobweb weavers (Table 5). Models combining the biomass of branch wood and foliage, branch horizontal spread and the abundance of prey explained as much as 66% and 48% of the variation in spider species richness and diversity, respectively (Table 5).

Selected habitat variables did not appear to be strong predictors of the total abundance of potential spider prey. The best model combining biomass of wood and foliage explained only 16% of the variation in the abundance of total arthropods other than spiders. Similarly, with the exception of Psocoptera, numbers of the most abundant prey groups in tree canopies—aphids, adult Diptera and Collembola—could not be predicted with a great accuracy using the selected habitat variables (Table 5).

DISCUSSION

The number of spiders, their species richness, and diversity in tree canopies increased with what a human observer might subjectively label as "structural complexity" of the host-tree species. For example, needle-covered branches of western hemlock unarguably appear to be more complex than leaves of red alder, and, similarly, Douglas-fir with its longer needles and "bushier" branches could be classified as more complex than redcedar. Similar patterns have been observed elsewhere. For example, a higher spider abundance on foliage of red spruce than on balsam fir in east-central Maine suggests that the curved needles of red spruce provide a more complex and better habitat for spiders than flat needles of balsam fir (Jennings & Dimond 1988; Jennings et al. 1990). Stratton et al.
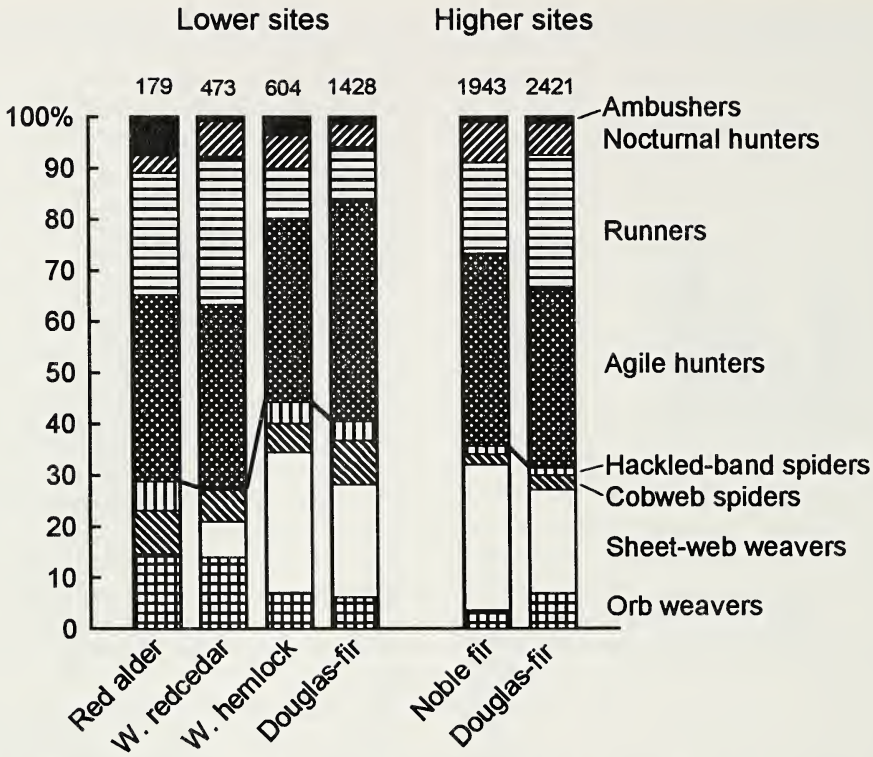
Figure 5.—Relative abundance of dominant spider groups on host-tree species at lower and higher-elevation sites. Numbers above columns indicate absolute densities of spiders collected from individual host trees. Solid lines between columns separate the web-building (below line), and hunting (above line) spider groups.

(1979) found higher spider densities and slightly more species on the more complex white spruce than white cedar in northern Minnesota.

Interestingly, the same host-tree species, Douglas-fir, supported a larger spider population at higher than lower elevations. Nocturnal hunters and running spiders in particular, were 2.8–4.6× more abundant on higher than lower-site Douglas-fir. A similarly high spider abundance was also observed on noble fir. This species, however, was not sampled at lower elevations, and so a direct comparison with other species is obscured by the "elevation" effect observed for Douglas-fir. A significant positive effect of altitude on arboreal spider abundance was also noticed by Russell-Smith & Stork (1994) in a tropical rain forest of Indonesia. Although no variables of spider habitat were measured in this study, it was suggested that differences in spider abundance could have been related to varying canopy architecture.

The term "plant architecture" was originally proposed by Lawton & Schröder (1977) to describe a wide array of plant structural attributes. Two main components of plant architecture are the size and the variety of above-ground parts. The size *per se* hypothesis predicts that larger plants (or habitat patches) are more likely to be discovered and colonized by arthropods, and consequently they support larger populations and a greater diversity of species (Lawton 1983). In addition, larger habitats generally have lower extinction and emigration rates (MacArthur & Wilson 1967; Kareiva 1985). The resource diversity hypothesis predicts that plants with a greater variety of structural variables or resource types (e.g., sites used for resting, sexual display, or feeding) support a greater abundance and diversity of arthropods (Lawton 1983).

On individual tree species, the greatest amount of variation in spider densities was explained by foliage biomass. Noble fir was an

exception, with prey availability being the critical variable. Similarly, from 60% to almost 70% of spider abundance across several host-tree species was related to branch biomass; either in the form of wooden twig or foliage. A similar coupling between spider abundance and habitat availability has been reported from a variety of communities (Duffey 1974; Hatley & MacMahon 1980; Rypstra 1986; Gunnarsson 1988). For example, correlative and experimental studies have shown that Norway spruce branches containing more foliage biomass support significantly more spiders than those with a reduced needle density in forest communities of southern Sweden (Gunnarsson 1988, 1990). Rypstra (1986) has documented strong correlations between the abundance of web-building spiders found on undergrowth vegetation and the biomass of this vegetation. Interestingly, this pattern was consistent across three distinct communities, ranging from tropical Gabon through subtropical Peru to temperate sites in the northeastern United States. This strongly suggests that spider abundance in tree canopies closely follows the availability (amount) of habitat substrate provided by host-tree species. Then, for example, although western hemlock appears structurally more complex than red alder, the disparity in the number of spiders that live on their branches may simply mirror differences in the branch biomass that both tree species can produce. Similarly, a greater spider abundance on higher-elevation Douglas-fir may be attributed to a greater biomass availability on this species at higher than lower sites.

From 40–57% of variation in spider species richness and diversity was related to branch biomass. This may be yet another example of a species-area relationship as both spider abundance and diversity increased with the amount of branch biomass. Similarly, Duffey (1974) and Uetz (1975) uncovered strong correlations between species richness and the depth (amount) of forest litter in communities of wandering spiders. Total habitat availability alone, however, does not sufficiently explain observed patterns of spider abundance and diversity. After accounting for the effect of branch biomass, still more habitat variables such as prey availability, number of individual leaves, branching angles, or branch spread entered the prediction models. These may reflect fine-grained qualities of the habitat (microclimate, web-constructing sites or refugia), allowing a greater niche diversification and coexistence of more spider species. For example, Greenstone (1984) documented a strong positive relationship between the diversity of web-building spiders and vegetation structural diversity across several habitat types ranging from tropical meadow in Costa Rica to scrub sites in California.

To illustrate the above arguments, there were more spiders collected from Douglas-fir than noble fir at higher elevations; yet, noble fir branches of comparable length contained more biomass than Douglas-fir. Similarly, redcedar branches contained significantly more foliage biomass than western hemlock or Douglas-fir, but supported fewer spider species than either host-tree species. Prey availability, or subtle differences in the branching pattern, resulting in a more favorable microclimate, may be responsible for this discrepancy. Indeed, Douglas-fir branches at all higher elevation sites contained twice the number of total non-Araneae arthropods, and more than three times the densities of aphids than noble-fir branches; redcedar was the most prey-poor of all species (Fig. 4). A greater predation pressure by birds on more exposed flat branches of noble fir (lower vertical branch spread) can also be a factor reducing spider abundance on this tree species.

Despite differences in spider abundance between Douglas-fir and noble fir, spider communities on both tree species were very similar. Likewise, Douglas-fir branches at all lower elevations had significantly more spiders than western hemlock, and yet both species supported almost identical spider assemblages. Conversely, non-Araneae arthropod community (order level) on western hemlock and Douglas-fir were only 55–57% similar, and the community of Douglas-fir and noble fir at higher elevations overlap 66–77% (Halaj 1996). It appears that some underlying habitat characteristics common to all of these tree species, rather than similarities in their prey communities, are responsible for similarities in spider assemblage structure. All of these species are conifers with needles, which may be the critical habitat variable for some spider groups. For example, both absolute and relative densities of sheet-web weavers were greater on conifers with needles compared to red alder or redcedar. Some species, such as

Table 2.—Arboreal spider community structure in western Oregon. Spider densities are pooled numbers of individuals collected from host-tree species across all study sites.

	Red alder	Western red-cedar	Western hem-lock	Douglas-fir Lower sites	Higher sites	Noble fir
Agile hunters						
Oxyopidae						
Oxyopes scalaris Hentz 1845	2	15	37	71	3	1
Salticidae						
Eris marginata (Walckenaer 1837)		1	1			
Habrocestum sp. Simon 1876	1	1	1	1		
Metaphidippus aeneolus Curtis 1892	58	139	170	542	836	707
Metaphidippus albeolus Chamberin & Ivie 1941			2			
Metaphidippus sp. F. O. P. Cambridge 1901	3	2			1	1
Phidippus johnsoni (G. & E. Peckham 1883)		1				
Ambushers						
Thomisidae						
Coriarachne versicolor (Keyserling 1880)	1					
Misumena vatia (Clerck 1757)	8		16	11	15	5
Misumenops celer (Hentz 1847)	4	2	4	1	1	1
Xysticus gosiutus Gertsch 1933		1		5	9	8
Nocturnal hunters						
Anyphaenidae						
Anyphaena pacifica (Banks 1896)	2	12	10	25	36	15
Clubionidae						
Clubiona moesta Banks 1896			1			9
Clubiona trivialis C. L. Koch 1843	4	19	27	38	115	125
Gnaphosidae						
Sergiolus montanus (Emerton 1890)						2
Runners						
Philodromidae						
Apollophanes margareta Lowrie & Gertsch 1955		2	9	17	40	56
Philodromus oneida Levi 1951				5		1
Phiodromus rufus pacificus Banks 1898	21	103	37	95	223	106
Philodromus speciosus Gertsch 1934		1		4	3	1
Philodromus spectabilis Keyserling 1880	21	19	10	31	375	171
Philodromus sp. Walckenaer 1825		4				1
Tibellus oblongus (Walckenaer 1802)			1	1		
Cobweb spiders						
Theridiidae						
Argyrodes fictilium (Hentz 1850)			1			
Dipoena nigra (Emerton 1882)		2	2	31	2	1
Euryopis formosa Banks 1908	1					
Theridion aurantium Emerton 1915			1			
Theridion differens Emerton 1882		4		24	19	3
Theridion lawrencei Gertsch & Archer 1942		11	19	56	42	24
Theridion melanurum Hahn 1831						1
Theridion neomexicanum Banks 1901	4	1		1	7	2
Theridion sexpunctatum Emerton 1882	3	4	2			1
Theridion simile C. L. Koch 1836	1		1	4		2
Theridion varians Hahn 1831			1			2
Theridion sp. Walckenaer 1805	6	5	6	6	1	2

Table 2.—Continued.

	Red alder	Western red-cedar	Western hem-lock	Douglas-fir		
				Lower sites	Higher sites	Noble fir
Hackled-band weavers						
Dictynidae						
Dictyna olympiana Chamberlin 1919	10	2	25	53	33	29
Orb weavers						
Araneidae						
Araneus gemma (McCook 1888)				5	10	1
Araniella displicata (Hentz 1847)	19	22	16	50	140	57
Cyclosa conica (Pallas 1772)		8	5	7	2	2
Undetermined genus, sp. 1	4	6	5	3		6
Tetragnathidae						
Metellina curtisi (McCook 1893)		8		1		
Tetragnatha laboriosa Hentz 1850				1	7	
Tetragnatha versicolor (Walckenaer 1841)	2	4	1	17	12	4
Uloboridae						
Hyptiotes gertschi Chamberlin & Ivie 1935		15	15	6		
Sheet-web weavers						
Lyniphiidae						
Ceraticelus atriceps (O. P.-Cambridge 1874)			58	84	39	345
Pityohyphantes costatus (Hentz 1850)				3	32	16
Pityohyphantes rubrofasciatus (Keyserling 1886)			10	57	106	87	44
Neriene litigiosa (Keyserling 1886)			18	14	25	
Undetermined genus, sp. 1	1	3	30	94	319	100
Undetermined genus, sp. 2					1	
Undetermined genus, sp. 3			2		8	29
Undetermined	3	28	17	4	3	62

Table 3.—Overlap in spider community structure and similarity of spider species composition for pairwise within-site host-tree species comparisons as determined with the Schoener's index of overlap and Søren-sen similarity index, respectively. * Results of 9 pairwise between-site comparisons.

| Host species	Index	Lower sites				Higher sites
		Red alder	Western redcedar	Western hemlock	Douglas-fir	Noble fir
Red alder	Community	1	0.71–0.74	0.57–0.77	0.58–0.67	—
	Species	1	0.50–0.60	0.50–0.51	0.41–0.56	—
Western redcedar	Community	—	1	0.62–0.71	0.58–0.75	—
	Species		1	0.60–0.68	0.60–0.78	—
Western hemlock	Community	—	—	1	0.83–0.94	—
	Species			1	0.74–0.80	—
Douglas-fir lower sites	Community	—	—	—	1	—
	Species				1	—
Douglas-fir higher sites	Community	—	—	—	0.67–0.91*	0.81–0.91
	Species				0.71–0.81*	0.71–0.79
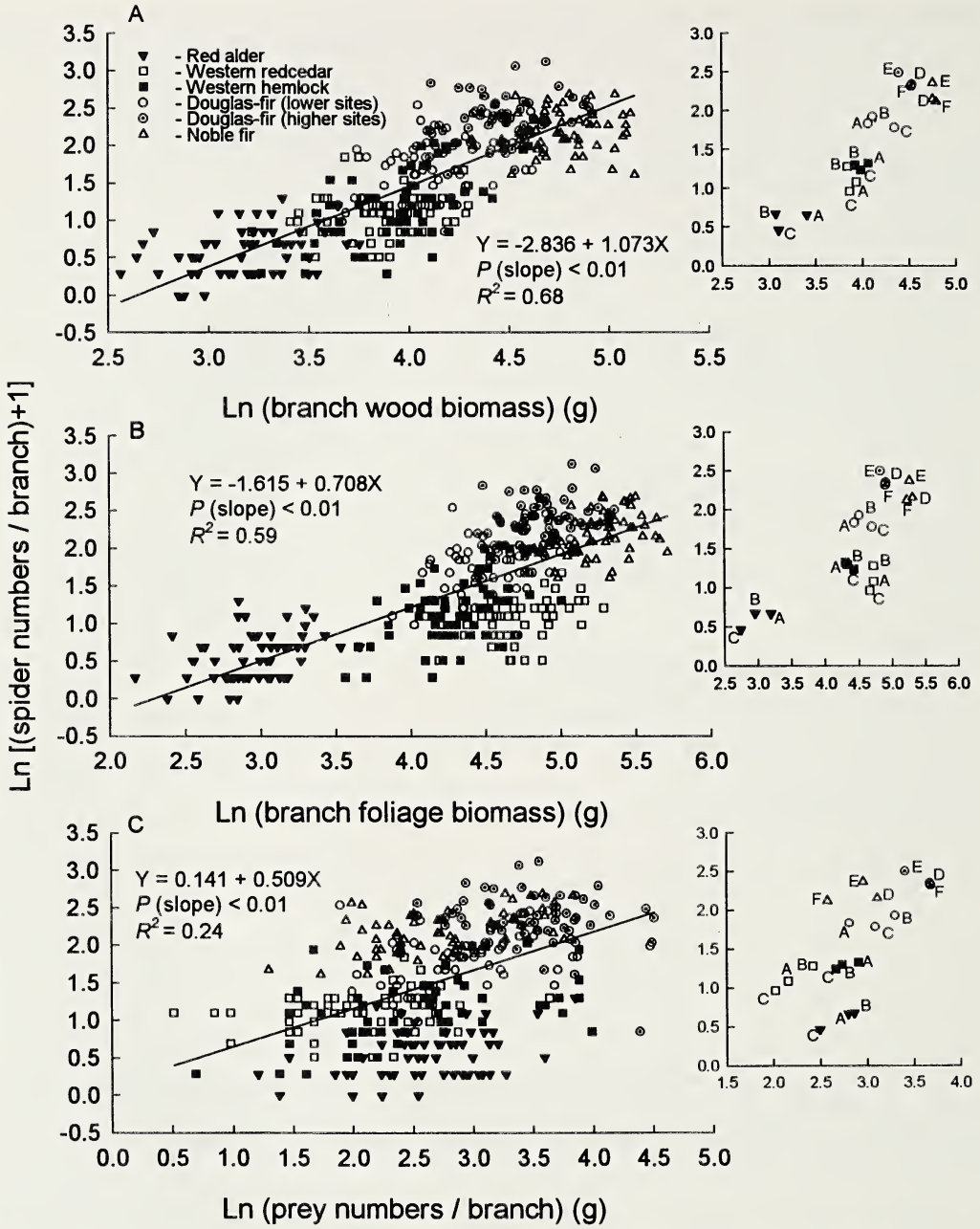
Figure 6.—The best prediction model for the total abundance of spiders in samples pooled across five host-tree species and six collecting sites. The model combines the branch wood biomass (A), branch foliage biomass (B) and the abundance of potential spider prey (C). Data points represent average variable values from three branches harvested on each tree ($n = 20$ trees, but $n = 17$ for red alder at site C). The inserts in the right portion of the graph display site averages.

Ceraticelus atriceps (O.P.-Cambridge 1874), were found exclusively on these hosts (Table 2). We commonly observed small linyphiids spinning their delicate webs around the base

of needles on Douglas-fir and western hemlock, and perhaps this habitat feature is essential to their foraging success. Similarly, Stratton et al. (1979) found a greater proportion of

Table 4.—Best models to predict spider densities on individual host-tree species in western Oregon. Y, spider density; DB, diameter at breast height; AG, number branching angles; HS, horizontal branch spread; VS, vertical branch spread; LF, number of leaves; FL, foliage biomass; WD, wood biomass; PY, prey density. * Amount of variation in the response variable explained by this variable alone as indicated by R^2. ** $P < 0.05$. *** $P < 0.01$.

Host species	Best model	$F\ (df)$***	R^2_{adj}
Red alder	$\ln(Y) = +LF +FL +PY$ $(0.13)\ (0.16)\ (0.13)*$	8.03 (3,53)	0.31
Western redcedar	$\ln(Y) = +\ln(FL) +\ln(LF)$ $(0.07)\quad (0.10)$	7.52 (2,55)	0.21
Western hemlock	$\ln(Y) = +\ln(FL) +\ln(PY)$ $(0.36)\quad (0.19)$	22.98 (2,56)	0.45
Noble fir	$\ln(Y) = +\ln(PY)$	25.28 (1,58)	0.30
Douglas fir lower sites	$Y = -\ln(DB) +\ln(VS) +\ln(FL) +\ln(AG)$ $(<0.01)\quad (0.05)\quad (0.22)\quad (0.15)$	9.79 (4,57)	0.45
Douglas fir higher sites	$\ln(Y) = +FL$	6.80 (1,57)**	0.11

linyphiids on red pine and white spruce compared to structurally simpler white cedar. Nevertheless, effects of community structure of potential spider prey on spider abundance and diversity deserve future investigations.

It has been generally accepted that structurally more complex habitats provide a wider selection of web-attachment sites and thus are more suitable for web-building spiders (Robinson 1981; Rypstra 1983; and reviews in Uetz 1991). Significant positive correlations between some groups of web builders and structural features of habitat in this study partly support this hypothesis (Table 5). With the exception of sheet-web weavers, however, correlations between densities of web-building spiders and habitat variables were weak. In addition, orb-weaving spiders did not appear to discriminate between red alder and western hemlock. Similarly, with the exception of lower-site Douglas-fir, cobweb spiders did not show a clear response in abundance to the complexity of individual host-tree species (Fig. 3). Some web-builders may be more flexible in utilizing the available habitat structure than others, and so a tight relationship between the abundance of these spiders and structural complexity of their habitat may not be universal principle. For example, orb weavers can spin webs across wider spaces in the canopy and their requirements for habitat complexity may be simpler, perhaps satisfied with a few attachment points. By the same token, it may be argued that our habitat variables did not precisely reflect fine-tuned habitat requirements of some web-builders, which may explain lower prediction power of our models. The abundance of hunting spiders also correlated with structural variables of their habitat. Increased amount and complexity of branch habitat may provide a greater assortment of retreat building sites and hiding places for hunting spiders (Hatley & Mac-Mahon 1980; Gunnarsson 1990). We commonly observed various hunters (Clubionidae, Salticidae and Philodromidae) in their diurnal and nocturnal retreats spun among needles on several host-tree species.

Higher densities of spiders were associated with increased densities of available prey organisms. This pattern was seen on individual host-trees species as well across several taxa. Correlative studies and field experiments have demonstrated spider numerical responses to prey densities (see review in Wise 1993) and our results further support these findings. Nevertheless, the prey variable generally explained less variation in spider abundance and diversity than the habitat alone. Individual spider groups may have specific prey requirements, and so it is conceivable that our broad prey category may not have been sensitive enough to detect stronger spider-prey associations. It is also plausible that food simply was superabundant in this system, thus precluding the detection of strong correlations.

Table 5.—Best models to predict densities of selected arthropod groups, spider species richness, and diversity across all host-tree species and sites in western Oregon. Variable codes as in Table 4. * Amount of variation in the response variable explained by this variable alone as indicated by R^2. ** $P < 0.01$.

Group	Best model	F (df)**	R^2_{adj}
	Density		
Araneae	ln(Y) = +ln(FL) +ln(WD) +ln(PY) (0.60)* (0.68) (0.24)	345.31 (3,341)	0.75
Agile hunters	ln(Y) = −ln(HS) +ln(WD) +ln(PY) (0.13) (0.49) (0.15)	129.73 (3,341)	0.53
Runners	ln(Y) = +ln(WD) +ln(PY) (0.34) (0.19)	116.73 (2,342)	0.41
Nocturnal hunters	ln(Y) = −ln(VS) +ln(FL) +ln(PY) (0.03) (0.21) (0.08)	41.82 (3,341)	0.27
Sheet-web weavers	ln(Y) = −ln(VS) +ln(WD) +ln(PY) (0.07) (0.44) (0.17)	114.63 (3,341)	0.50
Orb weavers	ln(Y) = +ln(VS) +ln(WD) +ln(PY) (<0.01) (0.09) (0.05)	14.80 (3,341)	0.12
Cobweb spiders	ln(Y) = +ln(HS) +ln(PY) (0.06) (0.04)	14.57 (3,342)	0.08
Total prey	ln(Y) = −ln(FL) +ln(WD) (0.05) (0.11)	31.38 (2,342)	0.16
Aphidoidea	ln(Y) = −ln(HS) −ln(FL) +ln(WD) (0.01) (<0.01) (0.02)	18.90 (3,341)	0.14
Psocoptera	ln(Y) = +ln(DB) +ln(HS) +ln(FL) −ln(WD) (0.27) (0.24) (0.21) (0.11)	46.99 (4,340)	0.36
Adult Diptera	ln(Y) = +ln(VS) +ln(WD) (0.01) (0.17)	43.42 (2,342)	0.20
Collembola	ln(Y) = +ln(DB) +ln(FL) −ln(WD) (0.11) (0.07) (<0.01)	34.27 (3,341)	0.23
	Species richness		
Araneae	ln(Y) = +ln(HS) +ln(FL) +ln(WD) +ln(PY) (0.36) (0.52) (0.57) (0.20)	164.23 (4,340)	0.66
	Diversity		
Araneae	ln(Y) = +ln(HS) +ln(FL) +ln(PY) (0.35) (0.40) (0.10)	105.00 (3,339)	0.48

For example, a 2.4-fold increase in prey availability following experimental removals of ants from Douglas-fir canopies did not translate into increased densities of web-building spiders at a nearby study site (Halaj et al. 1997). The relative importance of habitat structure and prey availability may also vary temporally as it was suggested for spider communities in forest litter (Uetz 1975) and agricultural crops (Rypstra & Carter 1995).

Structural complexity of habitat predicted the abundance of potential spider prey across several host-tree species. The availability of sites for oviposition, resting, basking, or overwintering is closely linked to plant architec-

ture (Strong et al. 1984); and thus both spiders and non-Araneae arthropods may respond to similar habitat features. Predicting the abundance of some groups (e.g., phytohagous species) based on their habitat architecture, however, may be difficult (Southwood et al. 1982). These groups are likely constrained by the nutritional quality of the host plant. Thus, a simple addition of habitat substrate, or an increase in its complexity, being heterogeneous in nutritional quality (e.g., habitat transition from alder to western hemlock), may not be followed by a strong corresponding increase in their abundance (Table 5).

In conclusion, this study documented sig-

nificant associations between the structure of branch microhabitat, prey availability, and the abundance and diversity of spiders in forest canopies. Nevertheless, these data should be interpreted with caution. Throughout the study, we assumed that plant biomass directly reflects the availability (surface area) of habitat to plant-dwelling arthropods. However, equal amounts of biomass may have different surface areas depending on the arrangement or fragmentation of the foliage. It is quite likely that an increase in plant biomass could indicate increasing surface area as well as the complexity of the host plant. Similarly, two host-tree species with equal surface area may differ in the weight of their branches if the densities of their plant tissue are different. Although most of the trends in arthropod abundance and spider community structure were strikingly similar at individual study sites, significant site*host-species interactions were present (Table 1, and throughout Results). This weakens the generality of our conclusions. Differences in the stand structure, modifying the site microclimate and composition of the herbaceous layer, may account for some of the discrepancies in the general trend. We suggest that colonization rates of habitats by dispersing arboreal spiders may reflect the patch size (habitat size *per se* hypothesis), and thus a greater abundance and more spider species would tend to accumulate on host-tree species whose branches provide more biomass. Subsequently, unique qualities of the host (e.g., local prey availability, branching complexity or microclimate; resource diversity hypothesis) perceived through various sensory channels would influence spider's decision to stay or leave a particular branch (e.g., see reviews in Riechert & Gillespie 1986). This would further modify differences in spider abundance and community structure across arboreal habitats. Due to the observational nature of this work, no cause-and-effect conclusions can be drawn. Experimental work is needed to ascertain the significance of specific features of spider habitat and prey availability, as well as temporal changes in their relative importance, as related to the abundance and community structure of these predators in forest canopies.

ACKNOWLEDGMENTS

LITERATURE CITED

Askenmo, C., A. von Brömssen, J. Ekman & C. Jansson. 1977. Impact of some wintering birds on spider abundance in spruce. Oikos, 28:90–94.

Cady, A.B. 1984. Microhabitat selection and locomotory activity of *Schizocosa ocreata* (Walckenaer) (Araneae: Lycosidae). J. Arachnol., 11: 297–307.

Coddington, J.A. & H.W. Levi. 1991. Systematics and evolution of spiders (Araneae). Ann. Rev. Ecol. Syst., 22:565–592.

Duffey, E. 1974. Habitat selection by spiders in man-made environments. Proc. 6th. Int. Arachnol. Congr., Amsterdam. Pp. 53–67.

Duffey, E. 1978. Ecological strategies in spiders including some characteristics of species in pioneer and mature habitats. Symp. Zool. Soc. London, 42:109–123.

Fichter, B.L. 1984. Arboreal arthropod predation on early instar Douglas-fir tussock moth. Ph.D. Thesis, Oregon State University, Corvallis.

Foelix, R. 1982. Biology of spiders. Harvard Univ. Press, Cambridge, Massachusetts.

Franklin, J.F. & C.T. Dyrness. 1988. Natural vegetation of Oregon and Washington. Oregon State Univ. Press.

Greenstone, M.H. 1984. Determinants of web spider species diversity: vegetation structural diversity vs. prey availability. Oecologia, 62:299–304.

Gunnarsson, B. 1988. Spruce-living spiders and forest decline: the importance of needle-loss. Biol. Conserv., 43:309–319.

Gunnarsson, B. 1990. Vegetation structure and the abundance and size distribution of spruce-living spiders. J. Anim. Ecol., 59:743–752.

Halaj, J. 1996. Abundance and community composition of arboreal spiders: the relative importance of habitat structure, prey availability and competition. Ph.D. Thesis, Oregon State University, Corvallis.

Halaj, J., D.W. Ross, R.R. Mason, T.R. Torgersen & A.R. Moldenke. 1996. Geographic variation in arboreal spider (Araneae) communities on Douglas-fir in western Oregon. Pan-Pacific Entomol., 72:17–26.

Halaj, J., D.W. Ross & A.R. Moldenke. 1997. Negative effects of ant foraging on spiders in Douglas-fir canopies. Oecologia, 109:313–322.

Hatley, C.L. & J.A. MacMahon. 1980. Spider com-

munity organization: seasonal variation and the role of vegetation architecture. Environ. Entomol., 9:632–639.

Jennings, D.T. & J.B. Dimond. 1988. Arboreal spiders (Araneae) on balsam fir and spruces in east-central Maine. J. Arachnol., 16:223–235.

Jennings, D.T., J.B. Dimond & B.A. Watt. 1990. Population densities of spiders (Araneae) and spruce budworms (Lepidoptera, Tortricidae) on foliage of balsam fir and red spruce in east-central Maine. J. Arachnol., 18:181–193.

Kareiva, P. 1985. Finding and losing host plants by *Phyllotreta*: patch size and surrounding habitat. Ecology, 66:1809–1816.

Lawton, J.H. 1983. Plant architecture and the diversity of phytophagous insects. Ann. Rev. Entomol., 28:23–39.

Lawton, J.H. & D. Schröder. 1977. Effects of plant type, size of geographical range and taxonomic isolation on number of insect species associated with British plants. Nature, 265:137–140.

Loughton, B.G., C. Derry & A.S. West. 1963. Spiders and the spruce budworm. Pp. 249–268, *In* The dynamics of epidemic spruce budworm populations (R.F. Morris, ed.). Mem. Entomol. Soc. Canada, 31.

Lubin, Y., S. Ellner & M. Kotzman. 1993. Web relocation and habitat selection in a desert widow spider. Ecology, 74:1915–1928.

MacArthur, R.H. & E.O. Wilson. 1967. The theory of island biogeography. Princeton Univ. Press, Princeton.

McIver, J.D., G.L. Parsons & A.R. Moldenke. 1992. Litter spider succession after clear-cutting in a western coniferous forest. Canadian J. For. Res., 22:984–992.

Moldenke, A.R., B.L. Fichter, W.P. Stephen & C.E. Griswold. 1987. A key to arboreal spiders of Douglas-fir and true fir forests of the Pacific Northwest. U.S. Dept. Agr., For. Ser. Gen. Tech. Rep., PNW-GTR-207.

Pielou, E.C. 1975. Ecological diversity. Wiley, New York.

Riechert, S.E. 1976. Web-site selection in the desert spider *Agelenopsis aperta*. Oikos, 27:311–315.

Riechert, S.E. & R.G. Gillespie. 1986. Habitat choice and utilization in web-building spiders. Pp. 23–48, *In* Webs, Behavior and Evolution (W.A. Shear, ed.). Stanford Univ. Press, Stanford.

Robinson, J.V. 1981. The effect of architectural variation in habitat on a spider community: an experimental field study. Ecology, 62:73–80.

Russell-Smith, A. & N.E. Stork. 1994. Abundance and diversity of spiders from the canopy of tropical rainforest with particular reference to Sulawesi, Indonesia. J. Trop. Ecol., 10:545–558.

Rypstra, A.L. 1983. The importance of food and space in limiting web-spider densities; a test using field enclosures. Oecologia, 59:312–316.

Rypstra, A.L. 1986. Web spiders in temperate and tropical forests: relative abundance and environmental correlates. American Midl. Nat., 115:42–51.

Rypstra, A.L. & P.E. Carter. 1995. The web-spider community of soybean agroecosystems in southwestern Ohio. J. Arachnol., 23:135–144.

SAS Institute. 1994. SAS User's Guide: Statistics. SAS Institute, Inc., Cary, North Carolina.

Schaefer, M. 1978. Some experiments on the regulation of population density in the spider *Floronia bucculenta* (Araneida: Linyphiidae). Symp. Zool. Soc. London, 42:203–210.

Schoener, T.W. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. Ecology, 49:704–726.

Schowalter, T.D. 1995. Canopy arthropod communities in relation to forest age and alternative harvest practices in western Oregon. For. Ecol. Manag., 78:115–125.

Southwood, T.R.E. 1992. Ecological methods (2nd ed.). Chapman & Hall, London.

Southwood, T.R.E., V.C. Moran & C.E.J. Kennedy. 1982. The richness, abundance and biomass of the arthropod communities in trees. J. Anim. Ecol., 51:635–649.

Steel, R.G.D. & J.H. Torrie. 1980. Principles and procedures of statistics: a biometrical approach. 2nd ed. McGraw-Hill, Inc. New York.

Stork, N.E. 1991. The composition of the arthropod fauna of Bornean lowland rain forest trees. J. Trop. Ecol., 7:161–180.

Stratton, G.E., G.W. Uetz & D.G. Dillery. 1979. A comparison of the spiders of three coniferous tree species. J. Arachnol., 6:219–226.

Strong, D.R., J.H. Lawton & R. Southwood. 1984. Insects on plants: community patterns and mechanisms. Harvard Univ. Press, Cambridge.

Sundberg, I. & B. Gunnarsson. 1994. Spider abundance in relation to needle density in spruce. J. Arachnol., 22:190–194.

Uetz, G.W. 1975. Temporal and spatial variation in species diversity of wandering spiders (Araneae) in deciduous forest litter. Env. Entomol., 4:719–724.

Uetz, G.W. 1991. Habitat structure and spider foraging. Pp. 325–348, *In* Habitat structure: the physical arrangement of objects in space (S.S. Bell, E.D. McCoy & H.R. Mushinsky, eds.). Chapman & Hall, London.

Wise, D.H. 1993. Spiders in ecological webs. Cambridge Univ. Press, Cambridge.

THE INFLUENCE OF HABITAT STRUCTURE ON SPIDER DENSITY IN A NO-TILL SOYBEAN AGROECOSYSTEM

Robert Andrew Balfour and **Ann L. Rypstra**: Department of Zoology, Miami University; Oxford, Ohio 45056 and Hamilton, Ohio 45011 USA

ABSTRACT. The goal of this research was to investigate the relationship between habitat structure and spider density in soybean fields managed under conservation tillage practices. Previous studies suggest that spiders respond to vegetational structure, and fields which are not tilled tend to have greater vegetational structure due to higher densities of weeds. Experimental subplots with varying densities of weeds (High, Medium, and Low weed) were established in soybean plots in southwestern Ohio. By the end of the season significantly more web spiders were found in treatments with higher weed densities. Across the season more than 87% of the spiders observed were orb-web weavers and sheet-web weavers. When considered separately, both of the common types of web spiders had higher densities in areas with higher densities of weeds. However, the degree to which orb and sheet-web weavers attached their webs to weeds differed across treatments. Orb-web weavers were more likely to attach their webs to weeds than to soybean plants or ground/ground litter in Medium weed density treatments. Sheet-web weavers were more likely to use weeds as a web attachment substrate in High weed density treatments.

A variety of studies have demonstrated a relationship between the structural complexity, or vegetational diversity, of a particular area and the abundance and/or diversity of web-building spiders (Colebourne 1974; Olive 1980; Robinson 1981; Rypstra 1986; Gunnarsson 1988, 1990; Döbel et al. 1990; Uetz 1991; Ward & Lubin 1993; Wise 1993; Pettersson 1996). Web spiders should be particularly sensitive to structural features of their environment because of the specific spatial requirements of web placement (Colebourne 1974; Riechert & Gillespie 1986; Uetz 1991). Indeed, experiments which changed existing features of a habitat, or added artificial substrate to which spiders could attach their webs, have demonstrated that spiders positively respond to such structural alterations (Robinson 1981; Rypstra 1983; McNett 1995).

The role spiders play in the food web and their potential as agents of biological control is becoming clearer (Riechert & Lockley 1984; Riechert & Bishop 1990; Young & Edwards 1990; Carter & Rypstra 1995). Conventional managment of agricultural fields leads to a structurally homogeneous environment which may minimize the abundance and diversity of spiders. However, in recent years, management practices designed to reduce erosion have become more popular in the United States, even though they lead to an increase in weed density and diversity (Gebhardt et al. 1985). The structural and microhabitat diversity provided by these weeds should enhance the web spider community and, in turn, may reduce the impact of pest insects. In a three year study, Rypstra & Carter (1995) found a positive correlation between spider density and weed biomass, and a negative correlation between spider density and herbivore damage in a soybean agroecosyem. Their study was purely correlative across fields and years so a more controlled investigation of the manner in which weeds may influence the spider community in a no-till agricultural system is warranted.

The goal of this study was specifically to relate weed density within no-till soybean fields to the abundance of web building spiders. Weed densities were manipulated in a replicate design and the web-spider community monitored across the season in order to test the hypothesis that the structural diversity provided by the weeds enhances spider abundance. In this way, we can begin to understand specifically how the changes in tillage practices implemented by American farmers may be impacting the other components of the biotic community that live in agroecosystems.

METHODS

Field work was conducted at Miami University's Ecology Research Center (ERC), located three miles northeast of Oxford, Butler County, Ohio USA. In 1995 we randomly se-

lected three of twelve 60 × 70 m (0.42 ha) soybean plots, planted in an east/west direction separated by 15 m corridors of mowed grass. Soybeans were planted on 6 June and three herbicides (Roundup™ (glyphosate, N-(phosphonomethyl) glycine in the form of its isopropylamine salt; 0.96 kg active ingredient/ha), Dual 8E™ (metolachlor; 2.03 kg active ingredient/ha), and Lorox Plus™ (linuron plus chlorimuron; 0.67 kg active ingredient/ha)) were applied pre-soybean emergence on 7 June. Two herbicides (Poast Plus™ (sethoxyoim plus dash; 0.23 kg active ingredient/ha) and Cobra™ (lactofen; 0.20 kg active ingredient/ha)) were applied post-soybean emergence on 11 July and 12 July, respectively, in conjunction with a crop oil concentrate/surfactant (2.34 kg/ha with Poast Plus™ and 1.17 kg/ha with Cobra™). The plots were not tilled at any time during the season.

Nine 1.0 × 1.0 m^2 subplots were placed within each of the 0.42 ha plots by generating coordinates on a 1 m grid using a random number table. Each subplot was at least 10 m away from any other and assigned to one of three weed density treatments: High, Medium, and Low weed densities. In subplots designated as Low, all weeds were manually removed weekly to maintain low weed structure. Subplots initially designated as Medium or High treatments were reassigned at the end of the field season depending on natural weed colonization in each subplot. Subplots with weed densities between 10–16 stems/ m^2 were assigned to the Medium treatment and 18–27 stems/ m^2 to the High treatment.

Data were collected every other week over a two month period, beginning on 25 July when the soybeans were in the mid-vegetative stage and ending 16 September, when the soybeans had senesced (Teare & Hodges 1994). We combined data for the first month (two sampling dates between 25 July–23 August) and refer to it as Early season. Similarly, we combined data for the second month (two sampling dates between 23 August–16 September) and refer to it as Late season. Early and Late season each consisted of two plant and two spider census samples. A mean value for each plot and treatment was calculated for both Early and Late seasons.

Quantification of plant structure.—Weed density was measured by placing a meter stick on the ground parallel to the soybean row,

touching the soybean stems. At two randomly chosen points along the length of that meter stick, another meter stick was placed on the ground perpendicular to the soybean row. The number of weed stems contacting the length of the second meter stick was recorded. Weed vertical structure was measured by dividing the subplots into four quadrats of 50 × 50 cm each. We selected two of these quadrats using pairs of random integers between one and four. At random locations within these chosen quadrats, a meter stick was positioned vertically and the number of weed leaves contacting its length was recorded. We calculated the vertical structure of the weed community by summing the number of weed leaves contacting the two meter sticks placed perpendicular to the ground. Soybean vertical structure was measured at the same two points as weed density, by holding a meter stick vertically in the soybean row and counting the number of soybean leaves in contact with the meter stick. We calculated the soybean vertical structure by summing the number of soybean leaves contacting the two meter sticks placed perpendicular to the ground. Weed and soybean height were calculated using the highest point a weed or soybean leaf touched the vertical meter stick.

Spider census.—Web spider density data were collected between 0730–0930 h when dew increased web visibility. First we searched each subplot for spiders on the vegetation and on the ground surface. Then we systematically inspected each plant starting at the base and moving upward. Each spider found was categorized according to its web type. Sheet-webs, (spun by Agelenidae, Linyphiidae), consisted of a horizontal sheet of silk sometimes bordered by a tangle of silk. Orb-webs, (spun by Tetragnathidae, Araneidae), were two-dimensional and mostly circular, with radii extending from the hub to the periphery. Any tangle or damaged webs we encountered were placed in a separate category. We also recorded the specific substrate to which each web was attached: ground/ ground litter (plant debris), soybean, weeds, or some combination of the three.

RESULTS

Quantification of plant structure.—Approximately seven species of weeds invaded the no-till soybean plots in 1995 (Table 1). Weed density per m^2 and weed vertical struc-

Table 1.—Common and scientific names of the most abundant weed species invading no-till soybean fields of southwestern Ohio in 1995.

Common name	Scientific name
Giant ragweed	*Ambrosia trifida*
Common ragweed	*Ambrosia artemisifolia*
Foxtail (grass)	*Setaria* sp.
Common milkweed	*Asclepias cyriaca*
Fescue (grass)	*Festuca elatior*
Ivy	*Convolvulus sepium*
Canadian thistle	*Cirsium arvense*

ture were significantly different among the three treatments in both time periods (Table 2). Weed height, soybean vertical structure, and soybean height did not differ between the three treatments in either season (Table 2).

Spider census.—Although in the Early season weed density had no effect on the density of spiders per m² (Table 3), there was a significant effect of weed density on spider abundance in the Late season (Table 3). Pairwise comparisons of the late season data suggest that there were significantly more spiders in High weed subplots than in Low weed subplots where weeds were removed (Duncan's New Multiple Range Test (DNMR), $P <$

0.05). If the data are uncoupled so each subplot and treatment are included, there is a significant correlation between the number of spiders and number of weed stems counted in subplots in the Late season ($r^2 = 0.356$, $P = 0.001$).

Orb-web weavers comprised 44% of the spiders censused both in the Early and Late seasons. The dominant orb-spinner in this system was *Glenognatha foxii* (McCook 1894) (Araneae, Tetragnathidae). In the Early season, the mean number of orb-webs per m² was not different among treatments; however, by the Late season there was a significant treatment effect (Table 3). Pairwise comparisons suggest High weed subplots had significantly more orb-weavers when compared to Low weed subplots (DNMR, $P < 0.05$). Orb-web weavers attached their webs to different substrates in different treatments ($\chi^2 = 16.74$, $df = 4$, $P < 0.005$, Fig. 1). More orb-webs were attached to weeds in Medium weed density treatments than in High or Low weed density treatments.

Sheet-web weavers comprised 43% of the spiders censused in both the Early and Late seasons. *Meioneta micaria* (Emerton 1882) (Araneae, Linyphiidae) was the dominant

Table 2.—Summary of vegetation structure within the experimental treatments (mean ± SE). Experimental treatments included High weed density (High), Medium weed density (Medium), and Low weed density (Low).

	High	Medium	Low	ANOVA results
Weed density per m²				
Early season	22.5 ± 1.2	11.8 ± 0.9	3.7 ± 0.1	$F = 105.7$, $df = 2$, $P < 0.05$
Late season	21.3 ± 4.5	16.0 ± 1.8	8.0 ± 0.8	$F = 5.48$, $df = 2$, $P < 0.05$
Weed vertical struc- ture (sum leaf number)				
Early season	42.0 ± 7.5	31.7 ± 3.7	5.7 ± 5.7	$F = 10.07$, $df = 2$, $P < 0.05$
Late season	53.5 ± 2.8	33.8 ± 7.0	0	$F = 38.46$, $df = 2$, $P < 0.05$
Soy vertical structure (sum leaf number)				
Early season	24.8 ± 3.6	22.2 ± 2.8	23.9 ± 1.0	$F = 0.228$, $df = 2$, $P > 0.05$
Late season	19.8 ± 2.1	20.3 ± 2.5	21.3 ± 2.0	$F = 0.110$, $df = 2$, $P > 0.05$
Soy height (cm)				
Early season	61.0 ± 3.4	61.8 ± 4.1	60.9 ± 4.2	$F = 0.016$, $df = 2$, $P > 0.05$
Late season	85.5 ± 1.8	80.7 ± 2.2	81.5 ± 1.9	$F = 1.799$, $df = 2$, $P > 0.05$
Weed height (cm)				
Early season	47.0 ± 6.1	44.5 ± 7.8	27.0 ± 2.0	$F = 1.480$, $df = 2$, $P > 0.05$
Late season	68.4 ± 8.1	48.2 ± 8.4	66.5 ± 17.0	$F = 1.532$, $df = 2$, $P > 0.05$

Table 3.—Summary of the total number of webs, subsequently broken down into sheet webs and orb webs, within the three weed density treatments (mean ± SE).

	High	Medium	Low	ANOVA results
Total number of webs per m²				
Early season	3.6 ± 0.5	4.7 ± 0.5	2.2 ± 0.7	$F = 3.564, df = 2, P > 0.05$
Late season	9.4 ± 0.6	7.1 ± 0.5	4.9 ± 1.3	$F = 5.914, df = 2, P < 0.05$
Number of sheet webs per m²				
Early season	1.6 ± 0.2	2.3 ± 0.7	1.3 ± 0.3	$F = 0.994, df = 2, P > 0.05$
Late season	5.0 ± 0.2	2.6 ± 0.4	2.1 ± 0.8	$F = 7.226, df = 2, P < 0.05$
Number of orb webs per m²				
Early season	1.6 ± 0.6	2.1 ± 0.9	0.8 ± 0.4	$F = 0.924, df = 2, P > 0.05$
Late season	4.0 ± 0.5	3.0 ± 0.4	1.5 ± 0.5	$F = 6.664, df = 2, P < 0.05$

sheet-web spinner in the fields. As was the case for orb-web spiders, we found no treatment effect on sheet-web weavers until the late season (Table 3). At that time, High weed subplots had significantly more sheet-weavers than Low weed subplots (DNMR, $P < 0.05$). Sheet-web weavers also utilized different web attachment sites as weed density changed ($\chi^2 = 14.91$, $df = 4$, $P < 0.005$, Fig. 2). Unlike orb-weavers, sheet-weavers were more likely to attach their webs to weeds in High weed subplots than in Low or Medium weed subplots.

DISCUSSION

The manipulation of weed density clearly affects the spider density in no-till soybean agroecosystems. We presume this relationship was due to differences in web support structures and/or the availability of appropriate microhabitats. Increased structural complexity has previously been correlated with spider abundance and diversity (Greenstone 1984; Rypstra 1986). Likewise, the addition of artificial web support structures has repeatedly resulted in an increase in web-spiders (Robinson 1981; Rypstra 1983; McNett 1995).
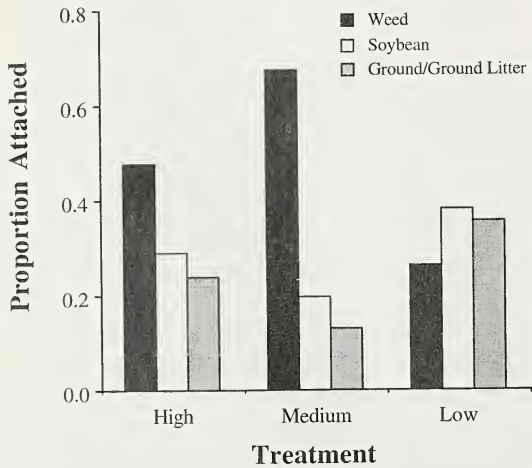

Figure 1.—The proportion of orb-webs attached to each substrate (weed, soybean, ground/ground litter) within each weed density treatment (High, Medium, and Low).
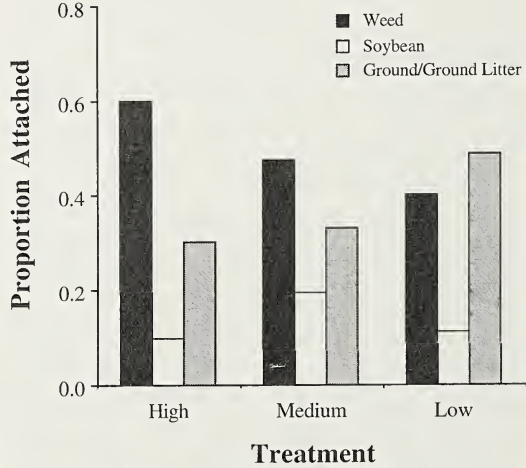

Figure 2.—The proportion of sheet-webs attached to each substrate (weed, soybean, ground/ground litter) within each weed density treatment (High, Medium, and Low).

Here we attempted to be as realistic as possible by monitoring the effects of natural plant invaders on web-spiders in an economically important habitat. These spiders rarely attached their webs to just one substrate as they would be forced to if we had used artificial constructs to alter the structural complexity available to them. Most of them used a combination of available plants, ground litter, and dirt as web substrates (Figs. 1, 2).

Difference in weed abundance not only changes the structural complexity of the environment but also ameliorates the microhabitat under the vegetation; especially near the ground surface. Most of the spiders surveyed were small (< 2 mm), and the majority of the webs were constructed on the lower third of the vegetation. Small spiders are more prone to dehydration than larger spiders due to their relatively high surface area to volume ratios (Pulz 1987). Building webs lower in the vegetation where there is increased humidity results in less direct exposure to sunlight, reducing the chance of dehydration. Also, a spider's ability to build an efficient capture web is maximized at certain thermal conditions (Barghusen et al. 1997), which may be present lower in the vegetation. Web destruction by wind is another factor affecting web site tenacity (Hodge 1987). The bases of plants provide sturdy support for web attachment and are less affected by wind.

If the high spider density in the presence of weeds was due to an increase in web supports, then one would predict that the spiders would be more apt to use weeds for web attachment in the weedier plots. In our plots, spiders tended to use the soil surface less and use weeds more as weed density increased (Figs. 1, 2). Although orb-web weavers used weeds to a high degree at Medium weed densities, they reduced their usage of this substratum in the High weed plots. It may be that orb-web weavers, who have very specific requirements for appropriate web placement, were responding more to microhabitat changes in the High weed treatments than to structural features. Once they established themselves in the plot, the regular spacing of the row of soybean plants may have offered a greater number of open spaces suitable for their planar webs. In a field study such as this, it is difficult to uncouple the relative role of structural complexity and microhabitat in producing the observed differences in web spider abundance.

The differences we observed in web substrate usage in response to weed density between sheet and orb-web weavers is intriguing and deserves further investigation.

Spiders are important generalist predators in terrestrial systems and no-till soybean agroecosystems are an increasingly important terrestrial habitat in the United States (Gebhardt et al. 1983). Rypstra & Carter (1995) demonstrated that spider density was positively correlated with weed biomass across years in conventionally tilled soybean fields. Typically, a reduction in tillage leads to an increase in weeds (Gebhardt et al. 1983). In this study, we demonstrated that, within one year, weed density in no-till soybean fields influenced spider abundance. These data contribute to our understanding of how shifts in agricultural practices may affect the spider community which may have larger implications for the productivity of the agroecosystem.

In the process of censusing for spiders it was necessary to disturb the vegetation within the subplots. The greater the vegetational structure within a subplot the greater the disturbance caused by the close visual inspection of the plants and soil surface. Therefore some spiders present in the subplots were probably overlooked due to web destruction. Since disturbance is related to the amount of vegetation, sampling error should have resulted in our values of spider density being underestimates in the Medium and High treatment subplots. Therefore any effects we report as significant would only be more striking if we had been able to find every spider.

Web spider density is increased by weed density presumably due to an increase in structural complexity. The close relationship we observed between weed density and spider density helps to explain the observed relationship between weed biomass and spider density Rypstra & Carter (1995) found across three seasons. Our work offers a greater understanding of how spider communities interact with the plant communities around them. It also offers us further insight into habitat selection by spiders and gives us a greater understanding of the animal community in agroecosystems.

ACKNOWLEDGMENTS

LITERATURE CITED

Barghusen, L.E., D.L. Claussen, M.S. Anderson & A.J. Bailer. 1997. The effects of temperature on the web-building behaviour of the common house spider, *Achaearanea tepidariorum*. Funct. Ecol., 11:4–10.

Carter, P.E. & A.L. Rypstra. 1995. Top-down effects in soybean agroecosystems: spider density affects herbivore damage. Oikos, 72:433–439.

Colebourn, P.H. 1974. The influence of habitat structure on the distribution of *Araneus diadematus* Clerck. J. Anim. Ecol., 43:401–409.

Döbel, H.G., R.F. Denno & J.A. Coddington. 1990. Spider (Araneae) community structure in an intertidal salt marsh: effects of vegetation structure and tidal flooding. Environ. Entomol., 19:1356–1370.

Gebhardt, M.R., T.C. Daniel, E.E. Schweizer & R.R. Allmaras. 1985. Conservation tillage. Science, 230:625–630.

Greenstone, M.H. 1984. Determinants of web spider species diversity: vegetation structural diversity vs. prey availability. Oecologia, 62:299–304.

Gunnarsson, B. 1988. Spruce-living spiders and forest decline; the importance of needle loss. Biol. Conserv., 43:309–319.

Gunnarsson, B. 1990. Vegetation structure and the abundance and size distribution of spruce-living spiders. J. Anim. Ecol., 59:743–752.

Hodge, M.A. 1987. Factors influencing web site residence time of the orb weaving spider *Microthena gracilis*. Psyche, 94:363–371.

McNett, B. 1995. Habitat Selection in the Silver Garden Spider *Argiope trifasciata*. Unpubl. master's thesis. Miami University, Oxford, Ohio.

Olive, C.W. 1980. Foraging specializations in orb-weaving spiders. Ecology, 61:1133–1144.

Pettersson, R.B. 1996. Effect of forestry on the abundance and diversity of arboreal spiders in the boreal spruce forest. Ecography, 19:221–228.

Pulz, R. 1987. Thermal and water relations. *In* Ecophysiology of Spiders. (W. Nentwig, ed.). Springer-Verlag, Berlin.

Riechert, S.E. & L. Bishop. 1990. Prey control by an assemblage of generalist predators: spiders in garden test systems. Ecology, 71:1441–1450.

Riechert, S.E. & R. Gillespie. 1986. Habitat choice and utilization in web building spiders. Pp. 23–49. *In* Spiders: Webs, Behavior, and Evolution. (W. Shear, ed.). Stanford Univ. Press, Stanford, California.

Riechert, S.E. & T. Lockley. 1984. Spiders as biological control agents. Ann. Rev. Entomol., 29:299–320.

Robinson, J.V. 1981. The effect of architectural variation in habitat on a spider community: an experimental field study. Ecology, 62:73–80.

Rypstra, A.L. & P.E. Carter. 1995. The web spider community of soybean agroecosystems in southwestern Ohio. J. Arachnol., 23:135–144.

Rypstra, A.L. 1986. Web spiders in temperate and tropical forests: relative abundance and environmental correlates. American Midl. Nat., 115:42–51.

Rypstra, A.L. 1983. The importance of food and space in limiting web-spider densities; a test using field enclosures. Oecologia, 59:312–316.

Teare, I.D. & H.F. Hodges. 1994. Soybean ecology and physiology. *In* Handbook of soybean insect pests (L.G. Higley & D.J. Boethel, eds.). Entomol. Soc. America; Landham, Maryland.

Uetz, G.W. 1991. Habitat structure and spider foraging. Pp. 325–348, *In* Habitat structure, the physical arrangement of objects in space (S.S. Bell, E.D. McCoy & H.R. Mushinsky, eds.). Chapman & Hall, New York.

Ward, D. & Y. Lubin. 1993. Habitat selection and the life history of a desert spider, *Stegodyphus lineatus* (Eresidae). J. Anim. Behav., 62:353–363.

Wise, D.H. 1993. Spiders in ecological webs. Cambridge Univ. Press, Cambridge, England.

Young, O.P. & G.B. Edwards. 1990. Spiders in the United States field crops and their potential effect on crop pests. J. Arachnol., 18:1–27.

LIFE HISTORY AND SOCIAL BEHAVIOR OF
ANELOSIMUS JABAQUARA AND *ANELOSIMUS DUBIOSUS*
(ARANEAE, THERIDIIDAE)

Evelyn S.A. Marques[1], **João Vasconcelos-Netto**[2] and **Maeve Britto de Mello**[2]:
[1]Laboratorio de Ecologia Evolutiva de Herbivoros Tropicais, Departamento de
Biologia Geral, ICB, UFMG, C.P. 486, CEP 30161–970, Belo Horizonte, M.G.,
Brazil; and [1,2]Dept. de Zoologia, Instituto de Biologia- C.P. 6109, UNICAMP, Barão
Geraldo - Campinas - S.P., CEP 13081–970 Brazil

ABSTRACT. The life history and social behavior of two sympatric spider species, *Anelosimus jabaquara* and *A. dubiosus* (family Theridiidae), were examined to provide comparative data of intermediate social behaviors in this genus of social spiders. Both species occur in sympatry in a subtropical humid lowland forest in Brazil and shared very similar life history traits such as univoltinism and slightly biased subadult sex ratios with more females per colony than males. Reproduction in *A. jabaquara* took place in early summer (December) and the brood developed during winter (April to October) under the care of females. But the reproductive periods in *A. dubiosus* and *A. jabaquara* were desynchronized by one month with *A. dubiosus* reaching maturity and mating in November. Both species showed cooperation in spinning and repairing the colonial web, in capturing prey and caring for the brood. When compared to *A. jabaquara*, in *A. dubiosus* there were 2.6× more individual spiders per colony, 1.4× more females than males, the colonial webs were 0.4× larger and the females showed greater cooperation in caring for the brood. We believe that *A. dubiosus* showed a more complex array of social behaviors when compared to *A. jabaquara* probably due to the greater tolerance of other conspecific individuals. We placed *A. jabaquara* in the same level of sociality as another non-territorial periodic-social species, *A. jucundus. Anelosimus dubiosus* would be a non-territorial permanent-social species in the same level of sociality as *A. domingo, A. rupununi* and *A. eximus,* but with less complex social behaviors than any of the former species.

RESUMEN. O ciclo de vida e o comportamento social de duas espécies de aranhas, *Anelosimus jabaquara* e *A. dubiosus* (familia Theridiidae), que ocorrem em simpatria em uma floresta subtropical húmida no Brasil, foram estudados para fornecer dados comparativos de comportamentos sociais intermediários neste gênero. Ambas espécies possuíam características de ciclo de vida muito similares, tais como: univoltinismo e razão sexual de subadultos ligeiramente desviada para mais fêmeas do que machos. A reprodução em *A. jabaquara* ocorre no início do verão (em dezembro) e a prole se desenvolve durante o inverno (de abril a outubro) sob o cuidado das fêmeas. Mas os estágios reprodutivos em *A. jabaquara* e *A. dubiosus* se encontravam desincronizados em um mês sendo que a reprodução em *A. dubiosus* se iniciou um mês antes—novembro- em relação à *A. jabaquara*. Ambas espécies mostraram cooperação na construção e reparo da teia colonial, na captura de presas e no cuidado à prole. Em *A. dubiosus* haviam 2.6× mais indivíduos por colônia, 1.4 mais fêmeas do que machos por colônia, as teias eram em média 0.4× maiores e as fêmeas mostraram maior cooperação no cuidado á prole quando comparada à *A. jabaquara*. Acreditamos que *A. dubiosus* tenha mostrado comportamentos sociais mais complexos quando comparada à *A. jabaquara*, provavelmente devido à maior tolerância de outros indíviduos da mesma espécie. Classificamos a espécie *A. jabaquara* como tendo um grau de socialidade similar ao de outra espécie não-territorial periódico-social *A. jucundus. Anelosimus dubiosus* foi classificada como uma espécie não-territorial permanente-social num grau de socialidade similar ao das espécies *A. domingo, A. rupununi* e *A. eximus,* mas com um grau de complexidade de comportamento social inferior aos das espécies anteriores.

Social behavior in spiders has originated independently in relatively few spider families (D'Andrea 1987, Avilés 1997). The existence of irregular webs that can be spun coopera-

tively by all individuals in a colony is an important preadaptation to the evolution of social behavior in spiders. This kind of web is typical for most the spider families that show

more complex social behaviors, such as Dictynidae, Agelenidae and Theridiidae. In such families another important adaptation would be the development of tolerance to conspecific individuals (Shear 1970).

The genus *Anelosimus* (Simon 1891) is of great interest because it contains solitary species as well as other species that show a gradient of social behaviors. This gradient is also exhibited in a few other species in the families Agelenidae, Dictynidae and Uloboridae; but *Anelosimus* has the largest number of social species known to researchers (Avilés 1997).

Avilés (1997) proposed a classification of social behaviors in spiders which is based on the length of time in which the spiders coexist as a colony (aggregation of individuals which live on the same nest and cooperate) and as to whether or not they maintain individual territories within the colony. Because spider species of the genus *Anelosimus* (Theridiidae) do not keep individual webs within a nest they can be grouped in two of the four categories: non-territorial permanent-social (quasisocial)—those species where "the adult members of a generation share a single communal nest and engage in cooperative prey capture and feeding"; non-territorial periodic-social (subsocial)—those species where "the siblings will continue to cooperate after the onset of maturity."

The species *A. eximus* (Keyserling 1891) has been classified as non-territorial permanent-social (Avilés 1997) and represents the pinnacle of sociality in the family Theridiidae (Vollrath 1986). The most important characteristics of its social behavior are: overlapping of two or more generations that cooperate in web spinning, in web maintenance and cleaning, prey capture and brood care; extremely biased sex ratios towards females, non-cooperative males and the existence of non-reproductive females (Vollrath 1982, 1986). Their colonial webs can contain up to tens of thousands of individuals and reach an area greater than 50 m^2 (Brach 1975; Christenson 1984; Vollrath 1983, 1986). There are four other species of *Anelosimus* which show less complex social behavior: *A. domingo* (Levi 1963) (Levi & Smith 1982; Rypstra & Tiery 1989), *A. rupununi* (or *A. lorenzo*) (Levi 1979) (Fowler & Levi 1979), *A. jucundus* (O.P. Cambridge 1895) (Nentwig & Christenson 1986) and *A. studiosus* (Hentz 1850)

(Levi 1963). The key adaptation to the evolution of social behavior in this genus seems to be an increase in tolerance of conspecifics followed by overlapping of generations which would allow more complex social behaviors to develop.

We studied two other species in this genus, *Anelosimus jabaquara* (Levi 1957) and *A. dubiosus* (Keyserling 1891), which coexist in sympatry and show similar life cycles and social behaviors. Our objective was to document the life history and social behavior of these two species with the expectation that it would produce some comparable data to aid in unveiling the steps in the evolution of social behaviors within this genus. Since the life histories of these species were unknown our first step was to document their biology and social behavior. Next we compared their social behaviors to those of other social species in the genus based on the available literature.

METHODS

This study was developed in the mountain range of Serra do Japí, in Jundiaí (23°11'S, 46°52'W), in São Paulo, Brazil. The colonial webs of both spider species occur on shrubs and trees of a subtropical humid lowland forest. Throughout this study we will use the word "colony" meaning the group of individuals that occupy a single web (colonial web) which was spun and maintained by these same individuals.

One trail of 1 km was marked at the elevation of 800 m and another at 1070 m above sea level. All the colonial webs found on these trails were individually marked in January and February of 1989. Measures of width, length and height were taken from each colonial web. Weekly observations were made, from January 1989 to March 1990, totaling 280 hours of field observations on the activity period of the colony, the number and stage of development of the spiders, the behaviors of web construction, prey capture and brood care.

One adult male and one female were collected from each colonial web for analysis of genitalia to distinguish between *Anelosimus jabaquara* and *Anelosimus dubiosus* (Levi 1963) and measured for the length of its cephalothorax. Voucher specimens were deposited in the Museum of Comparative Biology at Harvard University. We estimated the number
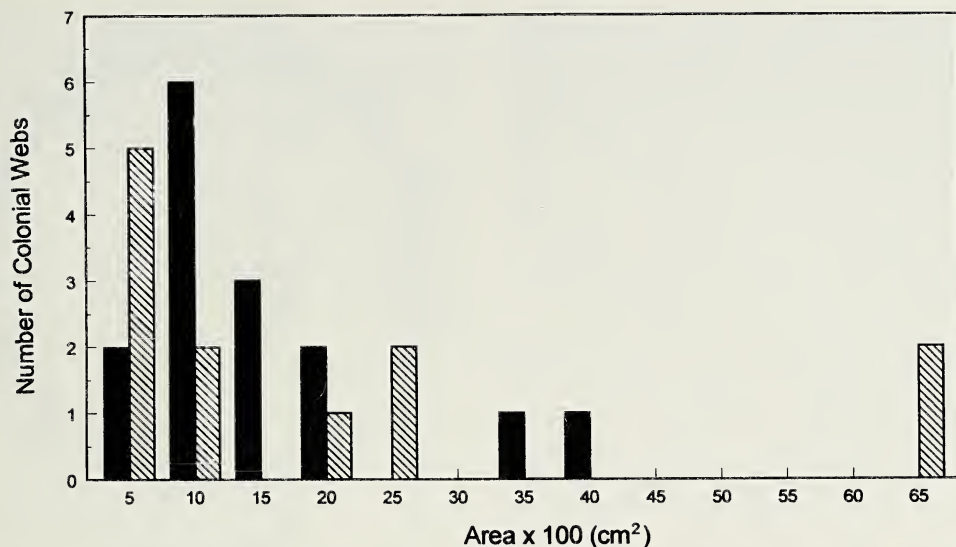
Figure 1.—Distribution of the sizes of the colonial webs of *Anelosimus jabaquara* (dark) and *Anelosimus dubiosus* (hatched) in the area of Paraíso I, Serra do Japí, Jundiaí, S.P., Brazil in December 1989.

of individuals in a web by throwing a Diptera (Tabanidae) inside the web and counting the spiders as they came out to feed. Since there was only one generation of brood in a web in one year it was possible to also record the stage of development and sex if they were close to the adult stages. The plant support was collected and all plant species occurring on a transect of 1 km long and 10 m wide were also collected for identification.

In January of 1989 three large colonial webs, with detritus and containing the mature brood of one or more females, were collected from both species and taken to the laboratory where they were put on plants of the family Myrtaceae in an open terrarium (1 m × 1 m), for detailed behavioral studies which totaled 100 hours of observations and for determination of stages of their life cycle. The egg sacs and all the molts found in the web were collected. These spiders were fed the Diptera *Ceratitis capitata* (Thephritidae).

From November 1989 through January 1990, 51 colonial webs with detritus were collected in the field, 41 webs of *A. jabaquara* and 10 webs of *A. dubiosus*. These colonial webs were taken to the laboratory were they were dissected to determine the identity of every single individual in the web, the number of egg sacs, the mean number of eggs per egg sac and the sex ratio of adults. A short manipulative experiment was conducted in the

field on five large colonial webs with detritus of each of the two species. In these experiments one adult female of *A. dubiosus* was dropped onto the sheet of the colonial web with adults of *A. jabaquara* (replicated five times) and one adult female of *A. jabaquara* was dropped onto the sheet of the colonial web with adults of *A. dubiosus* (replicated five times) and the behaviors of all adult spiders involved were noted.

RESULTS

Web structure.—The web structure for both species was very variable, and therefore it was not possible to distinguish between the two species based on the web alone. The colonial webs of *A. jabaquara* were usually shaped as a sheet over the branches and incorporated the leaves of the supporting plant. This "sheet" was made of a dense mesh of non adhesive threads spun in various directions on the same plane. The sizes of the colonial webs ranged from 20 cm^2 to 4000 cm^2 (mean area = 1437.5 cm^2, n = 16) (Fig. 1). This sheet functioned as a protection against any intruding natural enemy coming from underneath the web. Above this sheet there was an area that was made up of the leaves of the supporting plant surrounded by loosely spun non adhesive silk threads, "the retreat". The leaves served as shelter and the spiders were commonly seen hiding underneath these

leaves during the day. Above this area there were long adhesive silk threads spun vertically in the air and attached to the upper branches of the supporting plant; these were called the "threads to intercept prey" (see Brach 1975 for more details). The colonial webs of *A. dubiosus* were very similar to those of *A. jabaquara,* but usually the web was shaped as a basket instead of a sheet. The sizes of the colonial webs ranged from 100–6500 cm² (x̄ area = 2041.7 cm², *n* = 12) (Fig. 1).

Throughout this study we will be referring to two major types of webs: smaller webs, ranging in size from 1–150 cm², and characterized by new threads woven over green leaves and containing no detritus of any kind and the larger webs, ranging in size from 151–6500 cm², and containing considerable amounts of dead leaves and detritus. Approximately 88% of the colonial webs sampled were on plants of the family Myrtaceae while the frequency of occurrence of this plant family in this kind of vegetation was 15%. This was a significant difference and indicated a preference of these spiders for this family as a supporting plant for their webs (G = 289.01; *P* < 0.001; *n* = 92).

Life cycle.—*A. jabaquara* is a univoltine species with eight instars and the development of the colonies was synchronous. The reproductive period started in December and, at the population level, the first egg sacs were seen in the field in late January (Fig. 2). The spiderlings hatched and remained in the egg sac, going through their first molt inside the sac, sacs were present in the field for three months. The second and third stage or instar lasted one month each. The fourth instar, in the middle of the winter, lasted 3 months. The fifth instar lasted two months and with the arrival of the rains the sixth and seventh instar lasted approximately one month each. By early December the spiders had reached sexual maturity and started mating and caring for their egg sacs (Fig. 2).

Small colonial webs were originated by the dispersion of subadult individuals during the reproduction period and were easily identified in the field because these webs were always spun over the green leaves of the support plant and there were no detritus present in the form of dead leaves, dead prey or abandoned portions of web. The mean number of individuals on these new and smaller webs was 1.43 in-
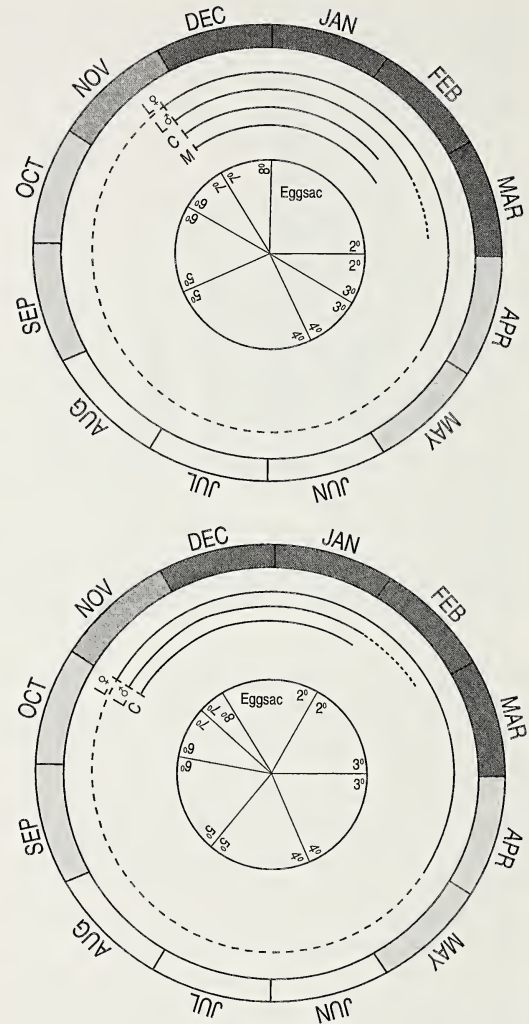

Figure 2.—Life cycle of the social spiders *Anelosimus jabaquara* (top) and *Anelosimus dubiosus* (bottom). The inner circle represents the duration of the life stages. The full lines represent the periods of copulation (C) and dispersion (M) and the longevity of males (L♂) and females (L♀). The outer circle indicates the rainy season (dark) and dry season (white).

dividuals per web (SD = ± 1.6; *n* = 32)(Table 1). The larger colonies were at least one year old because that was the minimum time needed for all the detritus to accumulate. The mean number of spiders in these larger colonial webs was 29.11 individuals (SD = ± 20.26, *n* = 9)(Fig 3).

Anelosimus dubiosus is also a univoltine species and showed a very similar life cycle to that of *A. jabaquara,* except that reproduc-

Table 1.—Composition of colonial webs resulting from dispersal of *Anelosimus jabaquara,* in December 1989, at Serra do Japi, Jundiai, S. P., Brazil. Females and males were present in subadult and adult stages of development.

Dispersing webs	Total number of individuals	Female	Males
1	1	1	
2	1	1	
3	1	1	
4	1	1	
5	2	2	
6	1	1	
7	1	1	
8	1	1	
9	1	1	
10	1	1	
11	1	1	
12	1	1	
13	1	1	
14	1	1	
15	1	1	
16	1	1	
17	1	1	
18	1		1
19	1		1
20	1	1	
21	1	1	
22	1	1	
23	1	1	
24	1	1	
25	1	1	
26	1	1	
27	1	1	
28	1		1
29	1		1
30	1	1	
31	1	1	
32	1	1	
Total	33	29	4

Table 2.—Composition of colonial webs resulting from dispersal of *Anelosimus dubiosus,* in January 1989, at Serra do Japi, Jundiai, S. P., Brazil. Females and males were present in subadult and adult stages of development.

Dispersing webs	Total number of individuals	Female	Males
1	1	1	
2	1	1	
3	1	1	
4	1	1	
5	9	9	
6	1	1	
7	1	1	
8	1	1	
9	1	1	
10	1	1	
11	1	1	
12	1	1	
13	1	1	
14	1		1
15	1		1
Total	23	21	2

(SD = ± 3.29; n = 15)(Table 2). The mean number of spiders in the larger colonial webs was 86.5 individuals (SD = ± 56.45, n = 6)(Fig. 3).

Daily activity period.—The activity period for both species was similar. The spiders remained under leaves inside the retreat during the hottest hours of the day (from 1000–1500 h). They stayed in a resting position with their legs retracted under the cephalothorax. At dawn and evening the spiders gradually left the retreat and started renewing the silk threads in the web or position themselves on the threads above the retreat and waited for prey to fall. In cold and rainy days the spiders were active all day long. Prey capture occurred in the daytime if the prey vibrated enough to attract the spiders causing them to leave their retreats to capture the prey.

Reproduction.—The reproductive period in *A. jabaquara* started in December when new colonial webs of single individuals or of a few number of individuals were found in the field. Field observations showed that three individuals, two females and one male, were observed dispersing through the vegetation by throwing threads into the air; and once the

tion started one month earlier, in November, and the first egg sacs were recorded in December (Fig. 2). The duration of the instars varied when compared to those of *A. jabaquara* and the whole phenology was one month ahead in time. At the population level the early instars of *A. dubiosus* also showed a considerably longer period of time for development in the dry season (winter) when temperatures were lower (30 °C). Smaller webs were also present resulting from dispersion with an average of 2.2 individuals per web
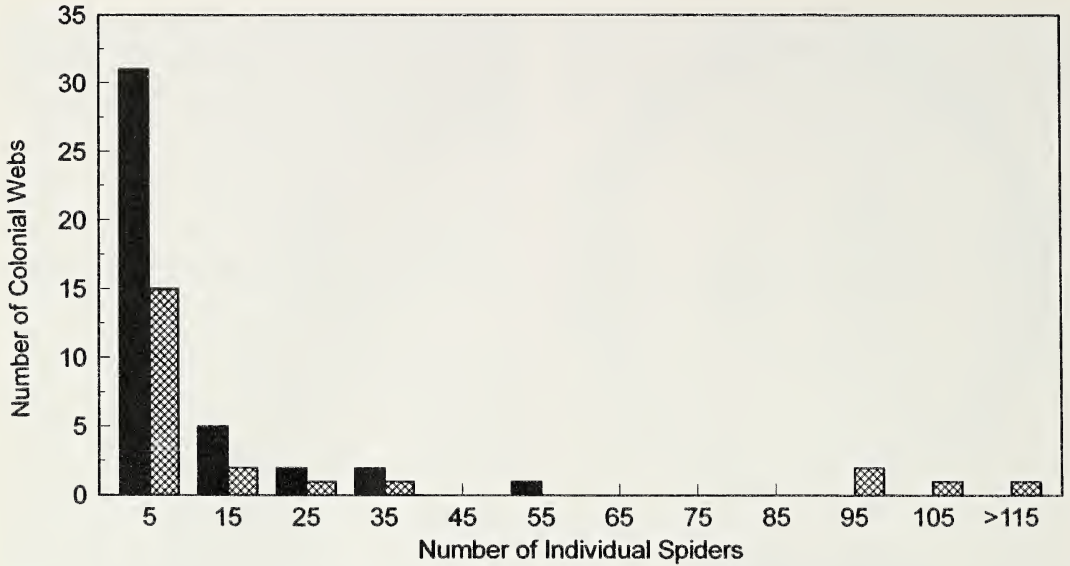
Figure 3.—Distribution of the number of individuals on colonial webs of *Anelosimus jabaquara* (dark) and *Anelosimus dubiosus* (hatched) in the area of Paraíso I, Serra do Japí, Jundiaí, S.P., Brazil in December of 1989.

threads attached to the vegetation, they would move to the next plant (these individuals were identified as *A. jabaquara*). These new colonial webs resulting from dispersion of subadult and adult individuals were very small and contained only green leaves in its structure and no dried leaves or other detritus. Once these colonies were established the marked females did not seem to leave their web unless the webs were greatly damaged. But field observations showed that unmarked males and, less often, females were seen entering and leaving established new colonies during this period (two males and one female).

Laboratory observations showed that two marked females were seen copulating with more than one individual male from the same web and four marked males were seen copulating with different females. Field observations showed that a female that was caring for its egg sac was seen leaving the egg sac to copulate with a male.

In the three colonies reared in the laboratory each of the 24 females laid at least one egg sac with approximately 27 eggs (SD = ± 8.06, $n = 34$)(minimum = 14 eggs; maximum = 49 eggs), being able to produce a second sac after abandoning their first. Approximately 25% ($n = 47$) of the egg sacs were unat-

tended and were either empty or had eggs parasitized by an unidentified microhymenoptera wasp. Other females that had their egg sacs experimentally removed tried to steal egg sacs from other females. Females that already had an egg sac or were caring for their brood were not seen laying a second egg sac.

Both in the field and in the laboratory females started dying in great numbers when their brood reached the 5th instar. Only one female survived until the brood reached the 7th or subadult instar. The males started dying soon after copulation and in January they were rarely seen in the field.

According to field observations the reproductive period in *A. dubiosus* started in November. Individuals of *A. dubiosus* were never found migrating in the field between webs, but we inferred that dispersion occurred because 14 small webs in the field contained single individuals and one small colonial web contained nine adult females (Table 3). In three larger colonial webs reared in terraria in the laboratory only one individual male of *A. dubiosus* ($n = 20$) dispersed and started a new web on a shelf, while all individuals ($n = 15$) of three colonies of *A. jabaquara* left the original web and dispersed, starting individual colonies on the shelves.

The males of *A. dubiosus* died in February

Table 3.—Composition of the sexes of colonial webs of *Anelosimus dubiosus* collected in the field from November (webs 1–5) and December (webs 6–10) of 1989, in Serra do Japi, Jundiai, S. P., Brazil.

Web #	Total number of individuals	Males	Females
1	18	4	14
2	17	4	13
3	15	0	15
4	10	6	4
5	104	34	70
6	18	4	14
7	20	8	12
8	12	1	11
9	20	2	18
10	95	15	80

and the females started dying when the brood was in the fourth instar. The mean number of eggs per egg sac in this species was 23.3 eggs (SD = ± 9.94, n = 38)(minimum = 5 eggs; maximum = 47 eggs). Only one out of six larger webs had parasitized egg sacs (2 sacs out of 47 sacs) by an unidentified microhimenopteran wasp.

In March of 1989 a total of 54 smaller webs from both spider species and resulting from dispersion (sizes ranging from 1–150 cm^2) had been marked and followed for 14 months. After 14 months 67% of the webs were abandoned and 17 of these colonial webs belonged to *A. jabaquara* and only one belonged to *A. dubiosus*.

Cooperation in brood care.—The males of *A. jabaquara* and *A. dubiosus* were not involved in brood care, probably because they were rarely present in the webs by then. Colonies collected in the field showed that adult males were usually smaller than adult females in *A. jabaquara* (mean male cephalothorax length = 1.38 cm, SD = ±0.004, n = 24; mean female cephalothorax length = 1.62 cm, SD = ±0.005, n = 25) as well as in *A. dubiosus* (mean male cephalothorax length = 1.4 cm, SD = 0.174, n = 9; mean female cephalothorax length = 1.64 cm, SD = ±0.126, n = 12). In both species the subadult sex ratio was biased towards females, in *A. dubiosus* it was 3.2:1 (females:males) (mean females per male per colony = 3.22, SD = ±0.21, n =

10)(Table 3) and in *A. jabaquara* it was 1.8:1 (females:males) (mean females per male per colony = 1.8, SD = ±0.21, n = 42) (Table 4). It was not possible to obtain the sex ratio of these spiders during the earlier stages of egg eclosion because the sex chromosomes in these species are microcromosomes and of difficult detection according to the Department of Cellular Biology of the University of Campinas.

In the field and laboratory, the females of *A. jabaquara* and *A. dubiosus* that were guarding their egg sacs moved very little and no new silk threads were added to the web during this period. The egg sacs were kept inside the retreat under leaves, and each female guarded its own egg sac.

Both in the field and laboratory the females of *A. jabaquara* rarely left the guard of their egg sac except when capturing prey or copulating and would return to their egg sacs immediately. The females inside their retreats could be as close as 10 cm from each other underneath different leaves or be touching each other while feeding. The females were very aggressive towards any conspecific female approaching its egg sac during reproduction. A female that was guarding its egg sac attacked any approaching female by touching the female with its front pair of legs, biting and pursuing it for a distance. A female, in the field, was seen gathering up to three other egg sacs besides her own under her retreat but when moving carried only one by the chelicerae. Another female, in the field, was seen feeding young spiderlings from a different brood (mother of the brood died) inside her retreat while caring for her own brood but that was only seen once.

Field observations show that spiderlings went through their first instar inside the egg sac. After they left the egg sac in their second instar they were gregarious staying with the female under a leaf in the retreat. The female showed the same protective behavior towards the brood as seen when it guarded the egg sac. The female fed her brood by what was believed to be regurgitation since the female would go to the retreat area and the spiderlings would all gather around the female's mouth area all at the same time. Four different adult females were seen feeding their brood by regurgitation until the spiderlings reached the third instar and were able to capture small

Table 4.—Composition of the sexes of colonial webs of *Anelosimus jabaquara* collected in the field from November (webs 1–12) and December (webs 13–41) of 1989, in Serra do Japi, Jundiai, S. P., Brazil.

Web #	Total number of individuals	Males	Females
1	60	27	33
2	57	31	26
3	14	8	6
4	31	14	17
5	34	14	20
6	45	25	20
7	55	19	36
8	47	5	42
9	41	16	25
10	32	9	23
11	39	16	23
12	40	3	37
13	59	33	26
14	23	13	10
15	35	10	25
16	22	14	8
17	14	9	5
18	71	59	12
19	10	5	5
20	89	42	47
21	21	6	15
22	56	19	37
22	11	5	6
23	49	21	28
24	27	14	13
25	47	21	26
26	40	19	21
27	17	11	6
28	21	12	9
29	11	6	5
30	42	18	24
31	17	7	10
32	35	18	17
33	78	35	43
34	46	27	19
35	12	4	8
36	20	11	9
37	20	10	10
38	18	10	8
39	18	11	7
40	12	8	4
41	35	8	27

prey on their own or would share the prey captured by the female. Around the fourth instar the juveniles of a brood mixed with those of other broods and the juveniles would either capture prey alone or in groups or eat prey captured by other females. Females started dying when the juveniles were in the fifth instar, while the males had died soon after copulation.

Field observations showed that the reproductive behavior of *A. dubiosus* was very similar to that of *A. jabaquara,* except that the females of *A. dubiosus* did not pursue the intruding females and were perceived as "less aggressive" towards each other and the broods of different females mixed in the second instar of their development. Each female of *A. dubiosus* guarded its own egg sac and would interact agonistically towards any approaching female by touching the front pair of legs and pulling the egg sac by the chelicerae. Intruding females were not pursued. In the second instar when the spiderlings had left the egg sac they mixed with spiderlings from other broods and any female in the web would feed the spiderlings by regurgitation. Older juveniles were also seen feeding the spiderlings by regurgitation. Females started dying when the brood had reached the fourth instar, while the males had died shortly after copulation.

Other social behaviors.—Both in the field and under laboratory conditions all the individuals, adult females and males (when present) and all spiderlings older than third or fourth instar, participated in the activities of web construction and repair, prey capture and occasionally removal of detritus. No significant difference was observed in the social behavior of the two species.

Web construction and repair: At dawn and evening all the individuals in the colonial web that were at the fourth instar or older in *A. jabaquara* and third instar and older in *A. dubiosus* left the retreat and started spinning silk threads in all directions with no apparent order. Some individuals started adding threads to the sheet while others spun threads at random over the retreat area. Still others spun threads up towards the leaves of higher branches. These individuals could switch activities anytime. This behavior enabled the spiders to add new threads to the web enlarging it as the individuals grew in size and also

to repair parts of the web that were damaged by rain, wind or animal activity.

Feeding behavior: In both species field observations showed that adult males and females participated in prey capture and that the bigger females (bigger abdomens) attacked the prey first by biting the thorax and abdomen of the prey. The smaller females (thinner abdomens) joined by biting the appendages or by turning their abdomen to the prey and releasing silk threads all over the prey with the aid of their last pair of legs. The females would then feed on the prey in groups or in the case of a smaller prey they would break the prey in parts and feed individually. After the prey had been immobilized by the females the males were seen biting the thorax and abdomen of the prey. The juveniles in their fourth instar helped the females in prey capture by biting the appendages of the prey. When the prey was not moving the juveniles would get on top of the prey and feed and the females would eventually abandon the prey, sometimes without even having eaten. The dead females were eaten by juveniles or other adult females in both species.

Removal of detritus: In both species the only objects removed by the spiders were empty egg sacs removed from the retreat area and thrown on the main sheet of the web.

Tolerance.—A short manipulative study revealed that when one adult female of *A. dubiosus* was dropped onto the sheet of the colonial web of adult *A. jabaquara,* the female at first would not move and when it moved it tried to escape from the web (all five trials). As soon as the individual of *A. dubiosus* moved, one or more females of *A. jabaquara* would approach and fight the intruding female, pursuing it until it had dropped from the web or had been killed. When one adult female of *A. jabaquara* was introduced in the web of adult *A. dubiosus* it would remain immobile for a few seconds and then go underneath a leaf; 30 minutes later two females were seen engaging in prey capture with the females of *A. dubiosus,* two others remained in the retreat and one dropped off the web.

DISCUSSION

The species *Anelosimus dubiosus* showed more complex social behaviors than its sympatric and conspecific species *A. jabaquara.* Both species showed the characteristics inherent to other social spiders in this genus. They inhabited colonial webs with more than a few individuals, these colonial webs would survive for more than one year and the subadult sex ratio was biased towards females. Nevertheless, *A. dubiosus* had larger colonial webs, with almost three times more individuals per colonial web and the sex ratio was skewed for 1.4 more females per male in a colonial web when compared with *A. jabaquara.* Despite the fact that we used subadult sex ratios, the end result was that there were potentially more reproducing females on colonial webs of *A. dubiousus* when compared to webs of *A. jabaquara.*

The dispersion of subadults and adults early in the reproductive season was very costly with a 67% mortality rate after 14 months, for newly established webs. Both species showed dispersion of subadults and adult males and females early in the season and the mean number of individuals on these dispersing colonies was slightly higher for *A. dubiosus.* From a total of 58 webs established at the beginning of the season, after 14 months only 18 webs had survived, 17 of those were *A. jabaquara* and one web was *A. dubiosus.* It is still not clear if the main mode of dispersion of *A. dubiosus* happens by the dispersion of single individuals or by budding off the main colony. There was no information available as to the initial species composition of the webs resulting from dispersion, but fewer of these smaller webs found in the field belonged to *A. dubiosus,* and no individuals of this species were found migrating in the field. Because one dispersing web had nine females, it is possible that this species utilizes both dispersing strategies. Since the mode of dispersion is crucial information to the understanding of phylogenetic relationships and population dynamics of social spiders, more detailed information is needed on the dispersion of *Anelosimus dubiosus.*

The most striking behavioral difference between these two species was related to the greater tolerance and cooperation observed in the brood care behavior of females of *A. dubiosus.* In both species females guarded their egg sacs, probably to protect them against predation, but the females of *A. dubiosus* would not guard their brood once they had emerged from the egg sacs. The spiderlings of different broods mixed and females or older juveniles

were seen feeding any brood by what appears to be regurgitation. This greater tolerance of other adult females allowed greater cooperation among females in the care of the young spiderlings which could have resulted in larger colonies containing the broods of several females.

Females of *A. jabaquara* guarded their egg sacs, as well as their broods, until the third instar and showed greater aggressiveness towards other conspecific females during the reproductive period. Even though we could not distinguish between cannibalism and predation of egg sacs for both species, we hypothesize that the greater aggressiveness towards other conspecific females was used as a means of protecting the egg sac and brood from cannibalism as has been documented for other *Anelosimus* (Christenson 1986). As a result of this aggressiveness there was less cooperation among females, colonies were usually smaller and more often contained the brood of one or a few females.

Another intriguing fact is that even though *A. jabaquara* and *A. dubiosus* are sympatric species utilizing the same plant families as support plants for their colonial webs (probably due to the alternate position of the leaves) and with a significant dispersion of individuals during reproduction, these species rarely mix. In our field samples we never found individuals of one species in the other species' colonial webs. This could be due to the differences in timing of reproduction, or more likely, a result of their chemical signaling which is very well known as the means of communication in spiders. Entering the wrong web and not being recognized (chemically) as an individual from that colonial web would certainly mean that you would be a potential prey specially for females of *A. jabaquara* (Smith 1989; Nentwig & Christenson 1986).

According to Avilés' (1997) classification, *Anelosimus jabaquara* can be considered as non-territorial periodic-social because its colony sizes are small ranging from 1 to 55 individuals, suggesting that these colonies were probably the result of the offspring of one or maybe two females that matured and reproduced. The greater aggressiveness towards conspecific females and the intense dispersion suggests that the colonies consists mainly of siblings. Another periodic-social species within the genus *Anelosimus* with similar life history and social behaviors would be *A. jucundus* (Levi 1963, 1976; Nentwig & Christenson 1986). *A. jucundus* showed many characteristics which are very similar to that of *A. jabaquara* such as: equal sex ratios, dispersion by subadult females and adult females, limited cooperation, aggression among females, one generation a year and usually smaller webs, even though a colonial web with up to 97 individuals was found (Nentwig 1986).

The colonies of *A. dubiosus* containing up to 176 individuals suggest that the brood of two or more cooperative females founded these colonies and therefore this species can be considered to be non-territorial permanent-social species. Based on Avilés's group selection hypothesis for permanent-social spiders we would expect *A. dubiosus* to have inbreeding isolated colonies much like the other permanent-social species. Even though this species has been shown to produce some migrating colonies of single individuals, these were few in number especially when compared with *A. jabaquara*; and there was also one new colonial web containing nine females which could be the result of budding off the main colony.

Anelosimus dubiosus had one characteristic in common with other non-territorial permanent-social *Anelosimus* species, *A. domingo* and *A. lorenzo* (Fowler & Levi 1979; Levi & Smith 1982): the greater tolerance among females and therefore greater cooperation in the activities of the colonial web. But the similarities end there because both *A. domingo* and *A. lorenzo* seem to have overlapping generations until the brood reaches adulthood, more than 1000 individuals per colony and sex ratios of up to 50 females per male. These characteristics resemble more those of *A. eximus* (Fowler & Levi 1979).

ACKNOWLEDGMENTS

Sierwald, Jim Berry and two anonymous reviewers for comments on the manuscript.

LITERATURE CITED

Avilés, L. 1997. Causes and consequences of cooperation and permanent-sociality in spiders. Pp. 476–498. *In* The Evolution of Social Behavior in Insects and Arachnids. (J.C. Choe & B.J. Crespi, eds.). Cambridge Univ. Press.

Brach, V. 1975. The biology of the social spider *Anelosimus eximus* (Araneae,Theridiidae). Bull. Southern California Acad. Sci., 74:37–41.

Christenson, T.E. 1984. Behaviour of the colonial and solitary spiders of the Theridiidae species *Anelosimus eximus*. Anim. Behav., 32:725–734.

D'Andrea, M. 1987. Social behaviour in spiders (Arachnida, Araneae). Italian J. Zool. N.S. Monogr. 3.

Fowler, H.G. & H.W. Levi. 1979. A new quasisocial *Anelosimus* spider (Araneae, Theridiidae) from Paraguay. Psyche, 86:11–18.

Kullman, E.J. 1972. Evolution of social behavior in spiders (Araneae, Eresidae, Theridiidae). American Zool., 12:419–426.

Levi, H.W. 1957. The spider genera *Neottiura* and *Anelosimus* in America. Trans. American Micros. Soc., 75:407–421.

Levi, H.W. 1963. The American spiders of the genus *Anelosimus* (Araneae, Theridiidae). Trans. American Micros. Soc., 32:30–48.

Levi, H.W. & D. Smith. 1982. A new colonial *Anelosimus* spider from Suriname (Araneae, Theridiidae). Psyche, 89:275–278.

Marques, E.S.A. 1991. Historia natural e comportamento social de *Anelosimus jabaquara* e *Anelosimus dubiosus* (Araneae; Theridiidae). Master's thesis, Univ. of Campinas, Brazil.

Nentwig, W. & T.E. Christenson. 1986. Natural history of the non-solitary sheet weaving spiders *Anelosimus jucundus* (Araneae, Theridiidae). Zool. J. Linn. Soc., 87:27–35.

Shear, F. 1970. The evolution of social phenomena in spiders. Bull. British Arachnol. Soc., 1:65–76.

Rypstra, A.L. & Tirey, L. 1989. Observations on the social spider *Anelosimus domingo* (Araneae, Theridiidae) in southwestern Peru. J. Arachnol., 17:368–370.

Vollrath, F. 1982. Colony foundation in a social spider. Z. Tierpsychol., 60:313–324.

Vollrath, F. 1986. Eusociality and extraordinary sex ratios in the spider *Anelosimus eximus* (Araneae, Theridiidae). Behav. Ecol. Sociobiol., 18:283–287.

THE ROLES OF PREY AND FLOWER QUALITY IN THE CHOICE OF HUNTING SITES BY ADULT MALE CRAB SPIDERS *MISUMENA VATIA* (ARANEAE, THOMISIDAE)

Susan A. Chien[1] and **Douglass H. Morse**[2]:   Department of Ecology and Evolutionary Biology, Box G-W, Brown University, Providence, Rhode Island 02912 USA

ABSTRACT.   Since adult male crab spiders *Misumena vatia* (Clerck 1757) (Thomisidae) feed sparingly and do not increase in mass, we wished to determine whether they responded to cues from hunting sites that would maximize their prospects of capturing prey. These spiders used cues from both prey and substrate as indicators of satisfactory hunting sites in the absence of females. They remained longer on red clover (*Trifolium pratense*) and ox-eye daisies (*Chrysanthemum leucanthemum*) in peak-condition flower than on senescent ones, and longer on daisies in peak-condition flower with prey than on peak-condition flowers without prey. They also remained as long on senescing daisies and clover with prey as on daisies and clover in peak-condition flower, but without prey. Thus, the effects of prey and substrate acted cumulatively on daisy, but not clover. However, they did not respond markedly differently on flowering and senescing branches of goldenrod (*Solidago canadensis*), although individuals on peak-condition flowers visited by prey remained somewhat longer than those at sites not visited by prey.

Current optimal foraging theory proposes that animals forage in a way that maximizes their rate of prey intake (Pyke et al. 1977; Morse & Stephens 1996). Adult male *Misumena vatia* (Clerck 1757) (Thomisidae) are particularly interesting in this regard since they do not increase in size during their adult stage (Gertsch 1939). The literature suggests that adult male spiders spend much of their time searching for females (Foelix 1996) or guarding penultimates prior to molt (Watson 1990; Dodson & Beck 1993), and they are often thought to take few or no prey during this period (Turnbull 1962; Vollrath 1987). We thus wished to establish whether precise hunting patch-choice behavior of adult male *Misumena vatia* would be reduced, relative to that of many other organisms whose individuals will grow rapidly at this time. This matter takes on added interest in that large females of this highly dimorphic (Gertsch 1939; Dondale & Redner 1979) species hunt voraciously and in some instances may increase in mass by as much as an order of magnitude as adults (Fritz & Morse 1985), a time during which they exhibit rather precise patch choice (Morse & Fritz 1982; Morse 1988).

In spite of these differences, male *Misumena* Latreille 1804 do hunt and capture prey in the field. We have observed that they frequently occupy flowers that attract nectar or pollen-seeking insects of a wide size and taxonomic range, including insects as small or smaller than male *Misumena*. We have also observed them with captured prey in the field, most often small Diptera ranging in size up to that of the spiders themselves. Further, they readily take prey in the laboratory. Thus, tests of flower choice should be both possible and realistic.

By testing the response of males to various hunting sites in the absence and presence of prey, we attempt to establish the importance of flower quality and prey presence in assessment of hunting sites by adult male crab spiders. We use giving-up times (Charnov 1976) as measures of site favorability. If male *Misumena* respond to predictions of this aspect of optimal patch choice theory (reviewed in Stephens & Krebs 1986), they should remain longer on high-quality flowers, even in the absence of prey, than on low-quality flowers, since high-quality flowers should eventually attract more potential prey than low-quality ones. (*Note:* This prediction depends on the ability of the males to evaluate flower condition in the absence of prey.) Quality may here be characterized by flower condition—nectar

[1]Current address: Dept. of Zoology, University of Florida, Gainesville, Florida 32711 USA
[2]To whom correspondence should be addressed.

producing or senescent. Also, male spiders should remain longer on a substrate, regardless of quality as defined here, if a prey item is present, than in its absence. Visiting prey should also provide cues to a good hunting site, since a substrate capable of attracting one prey is likely to attract more. Both cues could also combine to produce a maximum response.

METHODS

We conducted this study in a 1 ha field in Bremen, Lincoln County, Maine from June–August, 1993 and 1994. The site contained several species of flowering plants and is described in greater detail elsewhere (Morse 1981a; Morse & Stephens 1996).

Adult male crab spiders were collected from flowers along roadsides in Lincoln County, Maine (Bremen, Bristol, South Bristol). Upon capture, they were maintained in clear 7 dram plastic vials (5 cm high, 3 cm diameter) and fed small moths and flies every other day. We removed discarded prey items and cleaned the vials twice weekly. All experimental individuals retained at least three of their four raptorial forelimbs, typical of adults in the field. Other experiments with males have revealed no differences associated with the loss of a single forelimb (A.R. Holdsworth & D.H. Morse unpubl. data). We used the small (*ca.* 4 mg) syrphid fly *Toxomerus marginatus* (Say) (Syrphidae) for the prey presentations. This extremely common species (Morse 1979, 1981a, 1981b) is one of the most frequent prey taken by adult male *Misumena*, and by females as well (Morse 1979, 1995).

We used these spiders to run experiments on giving-up times, both 1) in the absence of and 2) in the presence of prey. To determine whether male spiders used flower quality alone as a cue in patch-choice decisions, we measured giving-up times of adult males in the absence of prey on high and low-quality red clover (*Trifolium pratense*), high and low-quality ox-eye daisy (*Chrysanthemum leucanthemum*), and high and low-quality goldenrod (*Solidago canadensis*). High-quality substrates were those whose flowers were in full bloom, and poor-quality substrates were those whose flowers had senesced. A close relationship exists between flower quality as here defined and numbers of visiting insects (Morse

& Fritz 1982). Spiders used in this experiment were not fed during the two preceding days, ensuring that they were in a similar non-satiated state (D.H. Morse unpubl. data).

We introduced each spider to the appropriate substrate by allowing it to climb onto a thin sable-hair brush and then slowly positioning the tip of the brush close to the flower until the spider climbed onto it. We terminated the experiment when the spider left the flower onto which it was introduced, or after 1 h. Tests were run only on clear or partly cloudy days between 0900–1700 h EDT. We did not monitor test flowers for previous insect visitation but refrained from using flowers containing spider silk from previous visitors.

We ran tests on clover and daisy using unscreened flowers, discarding tests if insects visited during the experimental period. This open-field test was quick and convenient, since insect visitors to the vicinity could almost always be chased from a surrounding flower before they would land on a focal flower. Spiders used in more than one experiment were never run on consecutive days, nor more than once in a particular experiment. All goldenrod experiments in the absence of insects were conducted in a large, walk-in screen cage (1.7 × 1.7 × 1.7 m) because the frequency of small insects on large inflorescences was so high that unscreened inflorescences seldom were without insects. Goldenrod inflorescences were thinned when in apposition to each other. High-quality branches were designated as those in which at least ¾ of the flower heads were in bloom. All of the flower heads had senesced on low-quality branches.

To assess the role of prey in determining patch choice, we tested in the same way the giving-up times of male crab spiders on the same flower species, to which small syrphid flies were introduced. We captured the syrphid flies used in the study with a large, open-mouthed jar (7 cm diameter, 17 cm height) that was slowly lowered over them as they fed at flowers. Flies were introduced onto test flowers within 5 min of the spiders, either by slowly lowering this upside-down jar containing syrphid flies over the flower until an individual climbed from the jar to the flower, or by slowly moving a fly from the jar on a sable-hair brush toward a test flower until it climbed onto that flower. The spiders did not respond to either the slowly-moving jar or
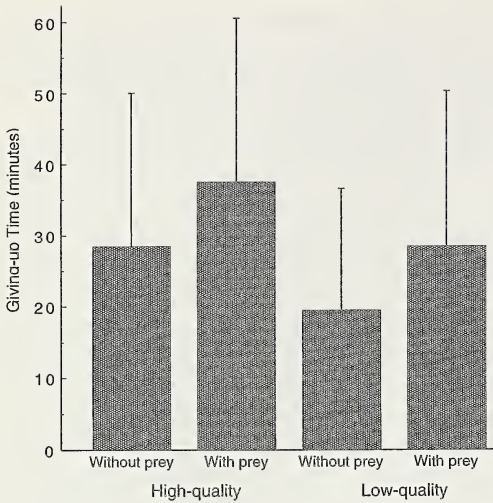
Figure 1.—Mean giving-up times ± 1 SD of adult male crab spiders on daisy (*Chrysanthemum leucanthemum*) inflorescences. Inflorescences at peak flowering (high quality) or senesced (low quality); single syrphid fly *Toxomerus marginatus* prey present or absent. *n*'s as in Table 1.
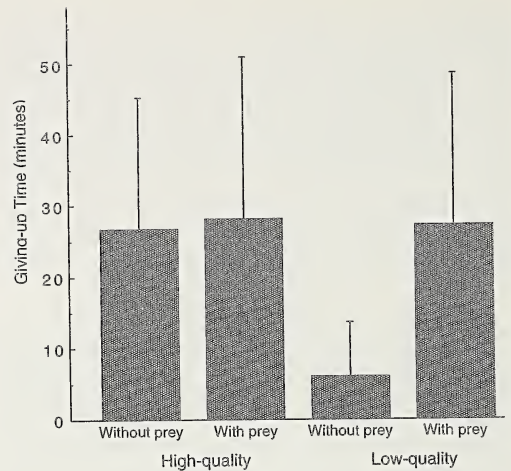

Figure 2.—Mean giving-up times ± 1 SD of adult male crab spiders on red clover (*Trifolium pratense*) inflorescences. Flower quality and prey as in Figure 1, *n*'s as in Table 1.

brush, so runs were combined. Runs were discarded if the spider left the flower before prey were successfully introduced or if the fly left the flower before the spider responded to it. Giving-up times were measured from the moment the fly elicited a response from the spider (orientation toward prey or movement toward prey). We also discarded the occasional runs in which the spider captured the prey. Specimens of *M. vatia* were deposited in the American Museum of Natural History.

RESULTS

Daisy.—A significant difference occurred among the experiments run on high and low-quality daisy inflorescences with and without prey (Fig. 1: $H = 13.65$, $df = 3$, $P < 0.01$ in a Kruskal-Wallis one-way ANOVA). Spiders on flowers without prey remained 1.5× as long on high-quality inflorescences as on low-quality inflorescences.

Introduction of prey to both high and low-quality inflorescences resulted in a nearly 50% increase in giving-up times over those without prey (Fig. 1). The difference between high and low-quality inflorescences with prey was also about 50%, with the result that low-quality inflorescences with prey exhibited giving-up times nearly identical to those of high-quality

inflorescences without prey. Thus, flower quality and prey acted in an additive way.

Clover.—A significant pattern also occurred among the experiments run on high and low-quality clover inflorescences with and without prey (Fig. 2: $H = 22.97$, $df = 3$, $P < 0.001$, same test). Spiders on flowers without prey remained over 4× as long on high-quality inflorescences as on low-quality ones.

Introduction of prey did not affect the time that spiders remained on high-quality clovers, but those on low-quality flowers remained over 4× as long if prey were introduced. However, giving-up times of spiders provided with prey on low-quality inflorescences were virtually identical to those of spiders in high-quality inflorescences, with or without prey introduction (Fig. 2).

Goldenrod.—No significant difference occurred among the experiments run on high and low-quality goldenrod inflorescences with and without prey (Fig. 3: $H = 6.71$, $df = 3$, $0.1 > P > 0.05$, same test). Spiders did remain 1.5× as long on high-quality goldenrod inflorescences with prey as on any of the other three choices, however, the only trend in the results (Fig. 3). Giving-up times of all three other experimental groups on goldenrod were virtually identical (Fig. 3). High-quality inflorescences without prey did not retain spiders any longer than low-quality inflorescences. Thus, the re-
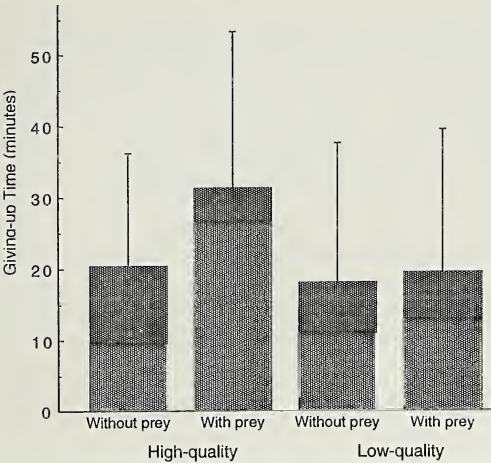
Figure 3.—Mean giving-up times ± 1 SD of adult male crab spiders on goldenrod (*Solidago canadensis*) inflorescences. Flower quality and prey as in Figure 1, *n*'s as in Table 1.

Table 1.—Percentage of individuals in different experiments that remained on an inflorescence one hour or more, with sample size in parentheses.

Species	No prey		Prey	
	High-quality	Low-quality	High-quality	Low-quality
Daisy	23 (30)	12 (26)	43 (28)	32 (25)
Clover	13 (15)	0 (16)	27 (15)	27 (15)
Goldenrod	6 (18)	7 (15)	28 (32)	13 (31)

sults for goldenrod differed somewhat from those of both daises and clover.

Variance.—In general the results all exhibited high variance, primarily the consequence of varying numbers of individuals remaining on an inflorescence for the entire 60 min of an experiment. Not surprisingly, numbers of spiders remaining 1 h or more differed among treatments and among flower species in a way that closely matched the results illustrated in Fig. 1–3 (Table 1). It is also important to note that in almost every instance the mean times portrayed in Figs. 1–3 are underestimates, since the experiments were terminated after 1 h (Table 1).

DISCUSSION

Under some circumstances adult male *Misumena* appear to use both flower quality and prey cues in assessing hunting sites. Daisies and clover both closely fit our original prediction that spiders would spend longer times on high-quality flowers than on poor ones. However, when prey were present, poor-quality daisies and clover retained spiders as long as high-quality clover in the absence of prey, demonstrating that more than one cue can serve as an indicator of good hunting sites. Although showing a qualitatively similar pattern, performances of the spiders nevertheless differed somewhat on the two flowers: the results from daisies suggested an additive effect of flower quality and prey; i.e., high-quality

sites with prey > high-quality sites without prey = low-quality sites with prey. In contrast, those from clover suggested a substitutive effect: high-quality sites with prey = high-quality sites without prey = low-quality sites with prey. This difference between the two flower species is most evident in the response to low-quality flowers without prey: senescent daisies without prey retain some attraction for the spiders, while one of the two characters is necessary to generate more than momentary adherence to clover.

Spiders did not clearly discriminate between low and high-quality goldenrod in the absence of prey, although they exhibited a modest trend to remain longer on high-quality goldenrod when prey were present than when absent. Thus, this male performance resembles that of adult female *Misumena* in the sense that flower quality does not play a significant role in choice of hunting site (Morse 1988). The role of prey as a cue for males on goldenrod thus remains tentative, though consistent with their responses on daisies and clover (Morse 1988).

Because daisies and clovers have compact inflorescences and goldenrod has much larger ones, the physical-temporal arrangement of prime flowers may be of major importance in accounting for differences in choice. Parts of a goldenrod inflorescence bloom asynchronously, so that some branches are in full bloom while others have not yet bloomed or have already senesced (Morse 1977). The spiders may thus have disregarded the flower quality of individual goldenrod branches, since a poor-quality branch may not characterize an entire inflorescence. If adjacent branches of the same inflorescences still attract prey, these prey may frequently land on a senescent branch occupied by a spider. This argument, however, fails to explain why spi-

ders showed no tendency to respond differently to the poor-quality inflorescences visited by prey.

In contrast, daisy and red clover inflorescences do not exhibit internal patchiness on the scale of the goldenrod. Individual clover inflorescences bloom and senesce within 10 days, and the ring of nectar-producing florets remains relatively constant over much of the life of a clover inflorescence (S.A. Chien pers. obs.); further, clover inflorescences are much smaller than goldenrod inflorescences. Therefore, spiders may assess a clover inflorescence in an all-or-none way; i.e., as one patch, while they assess a goldenrod inflorescence as a mosaic of patches. Our results suggest that where floral quality accurately reflects the ability to attract prey, male crab spiders will use flower quality independently as a cue for assessing the quality of hunting sites. This tactic would be potentially advantageous in allowing individuals to choose hunting sites when insect prey are not visiting flowers, thereby increasing considerably the period during which choices may be made.

These data establish that adult male spiders will respond directly to flower cues independently of the presence of females. The response to prey on daisies and clover demonstrates that they will react directly to another potentially critical resource—food—although the presence of prey should simultaneously increase the probability of finding females. Whether the increased time on sites with prey would be necessary to find such a female on a daisy or clover inflorescence seems questionable, judging from the short discovery times (a few sec to less than 5 min) exhibited in most male-female interactions we have staged on these substrates (A.R. Holdsworth & D.H. Morse unpubl. data). The similar attention of females to sites with prey simultaneously positions them on these favorable sites, enhancing probability of contact, even if the sexes do not actively search for each other. The giving-up times of males are all markedly shorter than those of either adult or penultimate-instar females, which appear to be involved totally in sit-and-wait foraging at such times (Morse & Fritz 1982; D.H. Morse unpubl. data). Males in the present study remained at high-quality sites for 1 h or more only 27–43% of the time (Table 1), far less than adult females, which remained over 2 h

at high-quality milkweed *Asclepias syriaca* inflorescences 69–80% of the time (Morse & Stephens 1996). Adult females also exhibited long tenure times on goldenrod and pasture rose, *Rosa carolina* (Morse 1981a).

ACKNOWLEDGMENTS

LITERATURE CITED

Charnov, E.L. 1976. Optimal foraging: the marginal value theorem. Theor. Popul. Biol., 9:129–136.

Dodson, G.N. & M.W. Beck. 1993. Pre-copulatory guarding of penultimate females by male crab spiders, *Misumenoides formsipes*. Anim. Behav., 46:951–959.

Dondale, C.D. & J.H. Redner. 1979. The crab spiders of Canada and Alaska. Araneae: Philodromidae and Thomisidae. Canada Dept. Agric., Res. Branch, Publ. 1663, pp. 1–255.

Foelix, R.F. 1996. Biology of spiders, 2nd ed. Oxford Univ. Press, New York.

Fritz, R.S. & D.H. Morse. 1985. Reproductive success and foraging of the crab spider *Misumena vatia*. Oecologia, 65:194–200.

Gertsch, W.J. 1939. A revision of the typical crabspiders (Misumeninae) of America north of Mexico. Bull. American Mus. Nat. Hist., 76:277–442.

Morse, D.H. 1977. Resource partitioning by bumble bees: the role of behavioral factors. Science, 197:678–680.

Morse, D.H. 1979. Prey capture by the crab spider *Misumena calycina* (Araneae: Thomisidae). Oecologia, 39:309–319.

Morse, D.H. 1981a. Prey capture by the crab spider *Misumena vatia* (Clerck) (Thomisidae) on three common native flowers. American Midl. Nat., 105:358–367.

Morse, D.H. 1981b. Interactions among syrphid flies and bumble bees at flowers. Ecology, 62:81–88.

Morse, D.H. 1988. Cues associated with patch-choice decisions by foraging crab spiders *Misumena vatia*. Behaviour, 107:297–313.

Morse, D.H. 1995. Gains of biomass by penultimate-instar crab spiders *Misumena vatia* (Araneae, Thomisidae) hunting on flowers. J. Arachnol., 23:85–90.

Morse, D.H. & R.S. Fritz. 1982. Experimental and observational studies of patch choice at different scales by the crab spider *Misumena vatia*. Ecology, 63:172–182.

Morse, D.H. & E.J. Stephens. 1996. The consequences of adult foraging success on the components of lifetime fitness in a semelparous, sit-and-wait predator. Evol. Ecol., 10:361–373.

Stephens, D.W. & J.R. Krebs. 1986. Foraging theory. Princeton Univ. Press, Princeton, New Jersey.

Turnbull, A.L. 1962. Quantitative studies of the food of *Linyphia triangularis* (Clerck) (Araneae, Linyphiidae). Canadian Entomol., 94:1233–1249.

Vollrath, F. 1987. Growth, foraging and reproductive success. Pp. 357–370, *In* Ecophysiology of spiders. (W. Nentwig, ed.). Springer-Verlag, Berlin.

Watson, P.J. 1990. Female-enhanced male competition determines the first mate and principal sire in the spider *Linyphia litigiosa* (Linyphiidae). Behav. Ecol. Sociobiol., 26:77–90.

RESEARCH NOTE

THE COURTSHIP OF A KANSAS POPULATION OF
HABRONATTUS BOREALIS (ARANEAE, SALTICIDAE)

The *coecatus* group of the jumping spider genus *Habronattus* consists of 23 described species, all found in the Western Hemisphere (Griswold 1987). The structure of the palpi in the male is generally diagnostic (see Griswold 1987, figs. 187–188). The epigynum of the female includes a central, elongated bell-like structure (see Griswold 1987, fig. 113–115). Courtship in the *coecatus* group is poorly known, although perhaps better known than in some other groups. Most of the species in the group have modifications on the third leg of the male at the patella-tibia junction, and these are displayed to the female during courtship (Griswold 1976; Richman 1982; Cutler 1988). Of the five species previously observed, *H. coecatus* (Hentz 1846), *H. borealis* (Banks 1895), *H. brunneus* (Peckham & Peckham 1900), *H. captiosus* (Gertsch 1934) and *H. pyrrithrix* (Chamberlin 1924), several usually have relatively long courtships, with periods approaching 30 min not uncommon with *H. brunneus* and *H. pyrrithrix*. During this time the male crouches low with his front legs raised and the palpi lowered. The third legs are raised and lowered, usually alternately; the patellae are rotated in and out and are nearly touching each other at the beginning and end of the sequence. Because *H. borealis* lacks any modification of the third leg we thought that the courtship might be different from the other species. Maddison & Stratton (1988) indicated that specimens of *H. borealis* from Michigan did have a courtship more typical of the species group, but also would twitch the abdomen down and up during courtship, producing a buzzing or purring sound below 500 Hz. They also noted an alternate shuffling of the left and right third legs. However, our observations on specimens of *H. borealis* from Kansas seem to confirm the hypothesis that members of this population have a much faster courtship with much less embellishment

than the other four species, or *H. borealis* from Michigan.

Live specimens of *H. borealis* were collected during May 1990, 1991 and late April and May in 1992 and 1993, at the University of Kansas, Lawrence, Douglas County, Kansas. These were maintained in vials and small petri dishes at room temperature in the laboratory, both at the University of Kansas and at New Mexico State University. Specimens were fed leafhoppers and *Drosophila*. At New Mexico State University males were placed in plastic petri dishes first, followed by the female. This procedure was established as standard because some salticid females (although not usually *Habronattus* females) may attack males as prey if they are placed in the dish first. Observations were then made directly, and courtship details were recorded by notes made during the observations. A total of 25 males was observed in courtship with 19 virgin, 5 gravid and 5 penultimate females (16 males, 13 virgin, 5 gravid and 4 penultimate females observed at Lawrence and 9 males, 6 virgin females and 1 penultimate female at Las Cruces). The spiders were all preserved and voucher specimens deposited at the American Museum of Natural History (New York), the Florida State Collection of Arthropods (Gainesville) and at the Arthropod Museum, New Mexico State University (Las Cruces). A video film of *Habronattus borealis* courtship made by Wayne Maddison and Gail Stratton using specimens collected in Michigan was analyzed and compared with our observations of this species from Kansas.

Specimens of *H. borealis* from Franconia, Grafton County, New Hampshire (type series in Museum of Comparative Zoology); Bergen County, New Jersey; Suffolk County, New York; Berrien County and Emmet County, Michigan; and Niagara County, Ontario, Canada, were compared morphologically with specimens from Douglas County, Kansas.

Epigyna of representative females from the Kansas population were removed and examined from both ventral and dorsal aspects. All appeared to belong to the same species based on morphology.

Other midwestern USA records of *H. borealis* (Bruce Cutler Collection) include ILLINOIS: 1♀, Cook County; KANSAS: 2♀ (penultimate) & 2♂ (males matured in laboratory), Chautauqua County; 2♂ & 2♀, Coffey County; 1♂, Wabaunsee County; and 1♂, Anderson County. Also 1♂ & 3♀ were examined from Morris County. NEBRASKA: 3♀ & 2♂ (penultimate), Saunders County.

Observed courtship displays were very short, usually over in 30–45 sec, often in shorter time. Only two courtships resulted in mating (one observed in Lawrence and one in Las Cruces), as the females, even when virgin, appeared to be highly resistant to male advances. Males often started tracking females before they saw them, sometimes drumming palpi on areas where females had been. Upon seeing the female, a male would raise its front legs, spread them 45°, elevate palpi about 45° and do a few (up to 3–4) brief zigzags, advancing toward the female, while moving the palpi up and down alternately. The female would typically raise her front legs as well. In all but two of the encounters, the male then jumped at the female; or, if the female advanced toward the male, he retreated. The first observations made us think that this might be accidental, the male mistaking the female for prey and becoming confused. However, in one trial the male went further. In this case the male turned upside down after jumping on the female and attempted to go under her from the front, with one palpus extended toward her epigynum. The female was able to push him off and retreat at this point. One male (collected 30 April 1993 and molted to maturity 10 May 1993) mated successfully at NMSU on 29 May 1993 with a female collected 4 May 1993 and matured 15 May 1993. This courtship was also very short, less than 30 sec in duration. In this case the female lowered her cephalothorax and allowed the male to climb over her and insert his palpus. The male alternately inserted his left palpus into the female's epigynum (2 min), shifted to the right (33 min) and then to the left (32 min). He then held on for another 4 min, as the female slowly turned. Finally they separated after 71 min.

Table 1.—Summary of courtship duration times (in seconds) for 33 trials of *Habronattus borealis* from Kansas. See text for details of type I and type II courtship.

	Type I	Type II	Type I and II	No display
Percent of total	42%	18%	18%	21%
Time	5–30	10–30	15–45	—

There seemed to be no opisthosomal bobbing as reported by Maddison & Stratton (1988) for Michigan *H. borealis*. Later attempts to get this same male to repeat his courtship with two other females resulted in the same sequence as seen in earlier courtships; *i.e.,* he jumped at the apparently very resistant, but virgin, females. A complete mating was also observed at Lawrence in 1993, but in this case no courtship was observed at all. The male over a period of about 1 min slowly approached the female from the rear, climbed on top with no interference from the female. After 30 sec the male turned around to face the rear of the female, tilted the female opisthosoma, and inserted his right embolus into the female epigynum. After 40 min, the male switched sides using his left palpus. After another 50 min, the female became active and the male shifted to full dorsal rear-facing position and released the female opisthosoma. The female moved or ran actively for 30 min, after which they broke apart. At least one female laid eggs after mating. One egg sac with 15 eggs was produced on 22 July 1993. Thirteen spiderlings hatched from this clutch on 24 August 1993, and a second egg sac with 9 eggs was produced 26 August 1996. It is not known whether the second egg sac hatched.

A summary of courtships observed is presented in Table 1. As in the observations described above, courtship was usually minimal. Type I courtship is initiated when the male is about 3 cm from the female, male zigzags, first leg raised about 45° and may be waved, palpi splayed to side and waving. Type II display initiated when male is about 1 cm from female, first legs raised at right angle to body, held somewhat forward, tarsi flicking down periodically, palpi elevated slightly and third legs may be shuffled.

The series of courtships filmed by Maddison & Stratton had a few early movements in

common with the Kansas population; the front legs spread and the palpi raised. However, the courtship continued and in at least one instance, prior to a male mounting a chilled or dead female, the male raised and lowered his third legs alternately, much as in other members of the species group. Maddison (pers. comm.) also observed a few courtships in the population of *H. borealis* from the Boston Mountains of Arkansas, as well as at least one courtship using a male from Kansas. He noted that type I courtship or type II courtship might be used, but he never saw both used by the same individual in the same courtship display. As in our observations, type I was used more than type II.

The Michigan males seem to have a courtship that is intermediate between the Kansas population and other members of the species group. The male bobs his palpi in unison and does use his third pair of legs in the display, despite the fact that there is no special ornamentation on the tibiae or patellae. As far as we can ascertain, the Kansas population has dispensed with this movement entirely. Even so, the Michigan courtship may be generally faster than reported in published records of the courtships of other members of the species group. It was difficult to be sure of this as the female filmed by Maddison & Stratton was apparently chilled, or dead.

Females of other species of *Habronattus*, including the members of the *coecatus* group in which courtship is known, have also been observed to be highly "resistant" to mating, even when virgin (Griswold 1976; Richman 1982). In these cases, however, the males continued courting for as much as a half-hour. The passivity of one female during one successful mating may point to a narrow window of physiological "readiness" in the Kansas populations. Even so, there was almost no courtship on the part of the male. The question now arises as to why the courtship of the Kansas populations has deviated so much from those of other members of the species group. On the other hand, why have at least some other members of the species group evolved such time-consuming and complicated courtships? Why spend up to a half-hour exposed

to possible predators or parasites while courting an apparently very resistant female? The question is a difficult one to answer and requires much more research.

LITERATURE CITED

Cutler, B. 1988. Courtship behavior in *Habronattus captiosus* (Araneae: Salticidae). Great Lakes Entomol., 21:129–131.

Griswold, C.E. 1976. Biosystematics of *Habronattus* in California. M.S. Thesis, Univ. California, Berkeley, 187 pp.

Griswold, C.E. 1987. A revision of the jumping spider genus *Habronattus* F.O.P. Cambridge (Araneae: Salticidae), with phenetic and cladistic analyses. Univ. California Pub. Entomol., 107:1–344.

Maddison, W.P. & G.E. Stratton. 1988. Sound production and associated morphology in male jumping spiders of the *Habronattus agilis* group (Araneae: Salticidae). J. Arachnol., 16:199–211.

Richman, D.B. 1982. Epigamic display in jumping spiders (Araneae, Salticidae) and its use in systematics. J. Arachnol., 10:47–67.

David B. Richman: Dept. of Entomology, Plant Pathology and Weed Science, New Mexico State University, Las Cruces, New Mexico 88003 USA

Bruce Cutler: Electron Microscopy Laboratory and Department of Entomology, University of Kansas, Lawrence, Kansas 66045 USA

RESEARCH NOTE

SOUGAMBUS GEORGIENSIS CHAMBERLIN & IVIE, A JUNIOR SYNONYM OF GONEATARA PLATYRHINUS (CROSBY & BISHOP) (ARANEAE, LINYPHIIDAE, ERIGONINAE)

Sougambus georgiensis Chamberlin & Ivie 1944 has not been collected since it was described from a series of females (Chamberlin & Ivie 1944). After trapping a female at Jackson, South Carolina which matched the description of *S. georgiensis*, I was hopeful that extensive pitfall trapping I was then conducting would turn up the male of the species. However, collecting a female in conjunction with males of *Goneatara platyrhinus* (Crosby & Bishop 1927) in Barnwell County, South Carolina suggested that these specimens could be conspecific.

The most direct method of demonstrating this putative synonymy, comparison of female type material of both species, is unfortunately not possible: the type material of *G. platyrhinus* (originally described as *Oedothorax* by Crosby & Bishop (1927) and subsequently transferred as the type of the new genus *Goneatara* by Bishop & Crosby (1935)) was never entered into the American Museum of Natural History (AMNH) type catalog when the Cornell University Collection was moved there. These types are presumed lost. No material from the type locality has been located at AMNH, although the specimens from the three other records listed in the description (Crosby & Bishop 1927) were found. Unfortunately, the female material in these vials is inadequate for definite comparison. A female was missing from a vial from North Carolina and a vial from Pennsylvania contained only a single female without an abdomen. A third vial referenced in Crosby & Bishop (1927), from Virginia, contained only males. A vial of two females collected in Mississippi by H. Dietrich in 1930 represents the only complete females of *G. platyrhinus* at AMNH. Because Dietrich and C.R. Crosby are sometimes listed as co-collectors of material in the Cornell University Collection, it might be assumed that Dietrich had access to authoritatively determined specimens of *G. platyrhinus*.

In the absence of female *G. platyrhinus* types, the synonymy of *S. georgiensis* and *G. platyrhinus* relies on several lines of evidence. First, the males and female I collected together appear to be the same species, with identical coloration including a characteristic "dusky short median stripe" (Crosby & Bishop 1927) or "median longitudinal patch of dark gray" (Chamberlin & Ivie 1944) on the abdominal dorsal surface. The males I collected appear identical to the *G. platyrhinus* material discussed above (again, *S. georgiensis* was described only from females). Male *G. platyrhinus* are easily recognized by the distinctive shape of the cephalic portion of the carapace (Crosby & Bishop 1927, figs. 3, 4), and their identity can be confirmed by details of palpal morphology (Crosby & Bishop 1927, figs. 1, 2). The rather simple epigynum figured by Crosby & Bishop 1927 (fig. 5) appears similar in form to the epigynum of *S. georgiensis* in Chamberlin & Ivie 1944 (fig. 114). Minor discrepancies in details of the two epigynal figures may reflect differences in artistic technique or differences in the pigmentation or sclerotization and hence transparency of the exoskeleton of the individual specimens drawn; some internal epigynal structures appear to be more distinctly visible in the Chamberlin & Ivie (1944) figure. The female I collected with the *G. platyrhinus* males appears identical to the holotype of *S. georgiensis* at AMNH and also to another specimen labelled "PARATYPE" but not designated as such in Chamberlin & Ivie (1944). It also matches the two females of *G. platyrhinus* collected and presumably determined by Dietrich, and the above mentioned abdomenless female *G. platyrhinus* listed in the original description (Crosby & Bishop 1927).

The striking similarity of the specimens examined strongly suggests that *Sougambus georgiensis* Chamberlin & Ivie 1944 should be considered a junior synonym of *Goneatara platyrhinus* (Crosby & Bishop 1927), even in the absence of female type material for *G. platyrhinus*. This emendation reduces *Sougambus* to a monotypic genus, with *S. bostoniensis* (Emerton 1882) as the only valid member (Platnick 1989, 1993).

Material examined.—Voucher specimens of males and females collected by the author have been deposited in the American Museum of Natural History. Following is the label data of all specimens examined. Material listed on the labels of some AMNH specimens has been lost. (AMNH) = American Museum of Natural History; (MD) = author's collection.

GEORGIA: Clarke County, Horseshoe Bend experimental area, floodplain forest, ethanol pitfall, 1♀, 26–27 February 1991 (M. Draney)(MD); N.E. Lula, 1♀, 26 April 1943 (W. Ivie) (AMNH) [PARATYPE (*S. georgiensis*)]. South of Guyton, 1♀, 5 April 1943 (W. Ivie) (AMNH) [HOLOTYPE (*S. georgiensis*)]. **MISSISSIPPI:** Richton, 2♀, 8 December 1930 (Dietrich) (AMNH) [labelled *Oedothorax platyrhinus*]. **NORTH CAROLINA:** Oteen, 1♂1♀, 16 October 1923 (C.R. Crosby & S.C. Bishop) (AMNH) [labelled *G. platyrhinus*]. **PENNSYLVANIA:** Roxbury, 2♀, 30 October 1924 (C.R. Crosby & S.C. Bishop) (AMNH) [labelled *G. platyrhinus*]. **SOUTH CAROLINA:** Aiken County, Jackson, deciduous woods behind 110 Cowden Street, pitfall, 1♀, 6–8 March 1995 (M. Draney) (MD). Aiken County, Savannah River Site, young pine stand at Road 2 and M-Line Railroad, formalin pitfalls, 3♂, 13–29 December 1995 (M. Draney) (MD). Same site, formalin pitfalls, 2♂, 10–24 January 1996 (M. Draney) (MD). Same site, formalin pitfall, 1♀, 17 April–4 May 1996 (M. Draney) (MD). Allendale County, Savannah River Site, Set-Aside #18, Boiling Springs Natural Area, riparian old-growth forest, formalin pitfall, 1♂, 29 November–13 December 1995 (M. Draney) (AMNH). Same site, formalin pitfalls, 2♀, 29 December 1995–10 January 1996 (M. Draney) (AMNH). Barnwell County, Savannah River Site, Set-Aside #29, scrub-oak/pine forest, formalin pitfall, 1♀, 1–15 May 1995 (M. Draney) (MD). Same site, formalin pitfalls, 2♂1♀, 11–28 December 1995 (M. Draney) (AMNH). Same site, formalin pitfall, 1♂, 22 January–6 February 1996 (M. Draney) (MD). Same site, formalin pitfall, 1♀, 4–18 March 1996 (M. Draney) (MD). Same site, formalin pitfall, 1♀, 1–16 April 1996 (M. Draney) (MD). Barnwell County, Savannah River Site, timber compartment

30, oak/hickory forest, litter extracted by Berlese funnel, 1♂, 4 November 1994 (M. Draney & D. Sanzone) (MD). Same site, formalin pitfall, 1♂, 28 December 1995–8 January 1996 (M. Draney) (MD). Same site, formalin pitfall, 1♂, 8–22 January 1996 (M. Draney) (MD). Same site, formalin pitfall, 1♂, 22 January–6 February 1996 (M. Draney) (MD). Same site, formalin pitfall, 1♀, 6–19 February 1996 (M. Draney) MD. Same site, formalin pitfall, 1♀, 19 February–4 March 1996 (M. Draney) (MD). Same site, litter sifting, 1♂4♀, 12 December 1996 (M. Draney) (MD) these five specimens were observed alive and reared in the laboratory; 2♀ (died 26 February 1997 and 6 April 1997) are preserved in separate vials]. **VIRGINIA:** Anna River, 2♂, 28 October 1923 (C.R. Crosby & S.C. Bishop) (AMNH) [labelled *G. platyrhinus*].

ACKNOWLEDGMENTS

LITERATURE CITED

Bishop, S.C. & C.R. Crosby. 1935. Studies in American spiders: miscellaneous genera of Erigoneae. Part I. J. New York Entomol. Soc., 43: 217–241, 255–281.

Chamberlin, R.V. & W. Ivie. 1944. Spiders of the Georgia region of North America. Bull. Univ. Utah, 35:1–267.

Crosby, C.R. & S.C. Bishop. 1927. New species of Erigoneae and Theridiidae. J. New York Entomol. Soc., 35:147–153.

Platnick, N.I. 1989. Advances in Spider Taxonomy 1981–1987: A Supplement to Brignoli's Catalogue of the Araneae described between 1940 and 1981. Manchester Univ. Press. 673 pp.

Platnick, N.I. 1993. Advances in Spider Taxonomy 1988–1991, with Synonymies and Transfers 1940–1980. New York Entomol. Soc. 846 pp.

Michael L. Draney: Savannah River Ecology Laboratory, Drawer E, Aiken, South Carolina 29802.

RESEARCH NOTE

WEB INVASION AND ARANEOPHAGY IN
PEUCETIA TRANQUILLINI (ARANEAE, OXYOPIDAE)

Although the majority of spider species may include other spiders in their diets, this practice generally is only an opportunistic occurrence. Some species, however, have specialized for prey exclusively or mostly on spiders, sometimes using very complex patterns of behavior, including the invasion of webs followed by the simulation of a trapped insect (Foelix 1982; Jackson 1992; Jackson & Hallas 1986). Routine predation on other spiders, called araneophagy, has evolved in distantly related groups, including Araneidae, Theridiidae, Gnaphosidae, Pholcidae, Archaeidae, Salticidae and Mimetidae (Stowe 1986; Jackson 1992). Some araneophagic spiders attack only a narrow range of prey, while others are adept at invading a wide range of web types and capture insects on their own webs.

Oxyopids are usually thought of as wandering spiders which chase prey (including other spiders opportunistically) on vegetation. Their ancestors, however, probably were web-building spiders (Rovner 1980) and at least one primitive genus (*Tapinillus*) builds webs (Griswold 1983; Griswold 1993). Studies related to the predation habits of oxyopids are almost restricted to two species: *Peucetia viridans* Hentz 1832 and *Oxyopes salticus* Hentz 1845; and almost nothing is known concerning neotropical species. Nyffeler et al. (1987) found, in a study in cotton fields, that about 40% of the prey captured by *P. viridans* were spiders, but all the records were made on vegetation, none on webs.

We observed individuals of *Peucetia tranquillini* Mello-Leitão 1922 invading webs and attacking males of *Nephila clavipes* Linnaeus 1767 during March and April 1996 at the Ecological Station of the Universidade Federal de Minas Gerais (Brazil). During the observations, from 0800–1800 h, we recorded nine *N. clavipes* web invasions. In addition, in 11 of 13 trials where *P. tranquillini* individuals were placed on vegetation close to *N. clavipes*

webs, the *P. tranquillini* spiders invaded the webs.

In only three instances did the intruders reach the spiral. In the others they moved slowly by anchor lines, taking their place in the frame until one of the residents moved (*Nephila* webs usually had a female and one or more males), vibrating the web. When this occurred, the intruder moved fast toward the source of vibration. In seven instances we observed attacks on the resident males. In two of them males were captured and carried to vegetation, while in three the intruder was attacked by the female (*Nephila* captured *Peucetia* only once). During one of these attacks on *Nephila* males, a *Peucetia* female apparently behaved as an aggressive mimic. That individual vibrated the web twice, once in the spiral (in which the *Nephila* female was attracted, resulting in the retreat of the *Peucetia*) and once in the frame threads (attracting a male which was attacked).

We also observed an invasion of a web of *Latrodectus geometricus* Koch 1841 (Theridiidae), where the intruder, an adult male, stayed for four days. During this time this individual captured insects which became caught in the web, and also stole prey that had been captured, wrapped up and set aside by the host spider. On another occasion we saw the invasion of a web of *Argiope argentata* Fabricius 1775 by another male of *P. tranquillini*, but it returned to the vegetation after reaching the spiral zone.

Dominant males of *N. clavipes* often react aggressively to vibrations at the edge of female web (Christenson & Goist 1979; pers. obs.), where the subordinate males usually stay. The web-vibrating behavior of *P. tranquillini* and the response of *N. clavipes* males suggest that *P. tranquillini* is capable of aggressive mimicry. However, it appears that in most cases *P. tranquillini* simply waits at the edge of the web for males to approach. Only

after more research will it be possible to say whether these species frequently practice araneophagy and web kleptoparasitism, and whether or not these forms of predation are associated with clearly specialized behaviors.

Voucher specimens were deposited at Instituto Butantan, São Paulo, SP (numbers IBSP 7380 and 7381).

ACKNOWLEDGMENTS

We wish to thank Lucia Garcia-Neto (Museu Nacional, RJ), for confirmation of the identification of *Peucetia tranquillini* specimens, Fernando A. Silveira and Hélcio R. Pimenta for suggestions on the manuscript. We also wish to thank the reviewers for their helpful comments.

LITERATURE CITED

Christenson, T.E. & K.C. Goist. 1979. Costs and benefits of male-male competition in the orb-weaving spider, *Nephila clavipes*. Behav. Ecol. Sociobiol., 5:87–92.

Foelix, R.F. 1982. Biology of Spiders. Harvard Univ. Press, Cambridge.

Griswold, C.E. 1983. *Tapinillus longipes* (Taczanowski), a web-building lynx spider from the American tropics (Araneae: Oxyopidae). J. Nat. Hist., 17:979–985.

Griswold, C.E. 1993. Investigations into the phylogeny of the lycosoid spider and their kin (Arachnida: Araneae: Lycosoidea). Smithsonian Contrib. Zool., 539:1–39.

Jackson, R.R. 1992. Eight-legged tricksters. BioScience, 42(8):590–598.

Jackson, R.R. & S.E.A. Hallas. 1986. Comparative biology of *Portia africana*, *P. albimana*, *P. fimbriata*, *P. labiata*, and *P. shultzi*, araneophagic, web-building jumping spiders (Araneae: Salticidae): Utilisation of webs, predatory versatility, and intraspecific interactions. New Zealand J. Zool., 13:423–489.

Nyffeler, M., D.A. Dean, & W.L. Sterling. 1987. Predation by green lynx spider, *Peucetia viridans* (Araneae: Oxyopidae), inhabiting cotton and woolly croton plants in east Texas. Environ. Entomol., 16(2):355–359.

Rovner, J.S. 1980. Did oxyopid spiders evolve from an aerial web-building ancestor? American Arachnol., 22:16. (abstract).

Stowe, M.K. 1986. Prey specialization in the Araneidae. Pp. 101–131. *In* Spiders: Webs, Behavior, and Evolution. (Shear, W.A., ed.). Stanford Univ. Press, Stanford, California.

Marcelo de Oliveira Gonzaga; Adalberto José dos Santos & Guilherme Fraga Dutra: Departamento de Zoologia - Instituto de Biologia - Universidade Estadual de Campinas. Caixa Postal 6109, CEP 13083–970, Campinas (SP) - São Paulo, Brazil.

RESEARCH NOTE

LEPTOPHOLCUS DELICATULUS (ARANEAE, PHOLCIDAE) IS A VALID NAME

Currently, only one species of the predominantly Old World genus *Leptopholcus* Simon 1893 is thought to occur in America: *L. dalei* (Petrunkevitch 1929), supposedly present both in Puerto Rico and in Cuba. The present paper shows that at least two species that were erroneously synonymized inhabit the two islands: the Puerto Rican *L. dalei* and the Cuban *L. delicatulus* Franganillo 1930. Only the Cuban species, which has never been illustrated, is treated in detail in the present note. *L. dalei* has been redescribed recently (Huber 1997) and is included only to the extent necessary for distinguishing the two species.

Leptopholcus delicatulus Franganillo 1930
(Figs. 1–21)

L. delicatulus Franganillo 1930: 59; ♀ lectotype (designated herein) and 5♀ paralectotypes, Cordillera de Guaniguanico: Sierra del Cuzco and Montañas de los Organos (Franganillo 1930), Cuba, IES (#208), vidi.

L. conicus Franganillo 1931: 286 (types probably lost, see note below); type localities: Cordillera de Guaniguanico: Sierra de Rangel, and Prov. Guantánamo: Baracoa (Franganillo 1931); Franganillo 1934: 153; 1936a: 46; 1936b: 78.

Micromerys dalei, -Bryant 1940: 296–297, 1♂ from Oriente: Los Llanos, and 1♀ from Pico Turquino (material probably lost, see Discussion).

Note.—The collection of P. Franganillo is currently deposited in the Instituto de Ecología y Sistematica, La Habana, Cuba. The vials are only numbered, contain no further labels, and the catalog is lost. This collection contains a single lot of adult *Leptopholcus* females, which we presume is the type series of *L. delicatulus* because this is the species described only from females, whereas *L. conicus* was described from males and females. There are no male *Leptopholcus* in the collection, and no further lots that could be assigned to *L. conicus*. Thus, we assume that the type material of *L. conicus* is probably lost. The assumption that the two species are synonyms is based first on our study of other material from several Cuban localities, including sites that are very near to the type localities of both species in the westmost and eastmost provinces (see below), and second on Franganillo's (1936b) own judgement (he erroneously gave precedence to the junior synonym, *L. conicus*).

Diagnosis.—Pale, medium-sized (about 4–5 mm total length) pholcid with long cylindrical opisthosoma. Most characters of *L. delicatulus* closely agree with *L. dalei* Petrunkevitch 1929 (see Petrunkevitch's (1929) detailed original description, and the redescription in Huber (1997) which also lists the type and non-type material of *L. dalei* studied by the first author and used for the present comparison). However, the distal processes of the procursus, an apophysis of the pedipalpal tarsus that is inserted into the female during copulation in all pholcids studied (review in Huber & Eberhard 1997) differ significantly, both in number and shape (Figs. 1, 2, 6, 7). The anterior median eyes are always clearly visible as vestiges in *L. delicatulus* (Fig. 3) with lenses of about 12–16 μm diameter (the other eyes measure 80–90 μm), while they are absent in *L. dalei* (Fig. 8). There seem to be some other minor differences, but these need to be tested on larger samples: in *L. dalei* the epigynum may be wider (Figs. 5, 10; but: Fig. 17) and the epigyneal knob larger (Figs. 4, 5, 9, 10), the carapace seems to be less round (Figs. 3, 8), the pedipalps may be relatively smaller, and the trochanter-apophyses may be more curved.

Redescription.—As stated above, the present species is very similar to the well described *L. dalei*. The present redescription thus concentrates on previously neglected
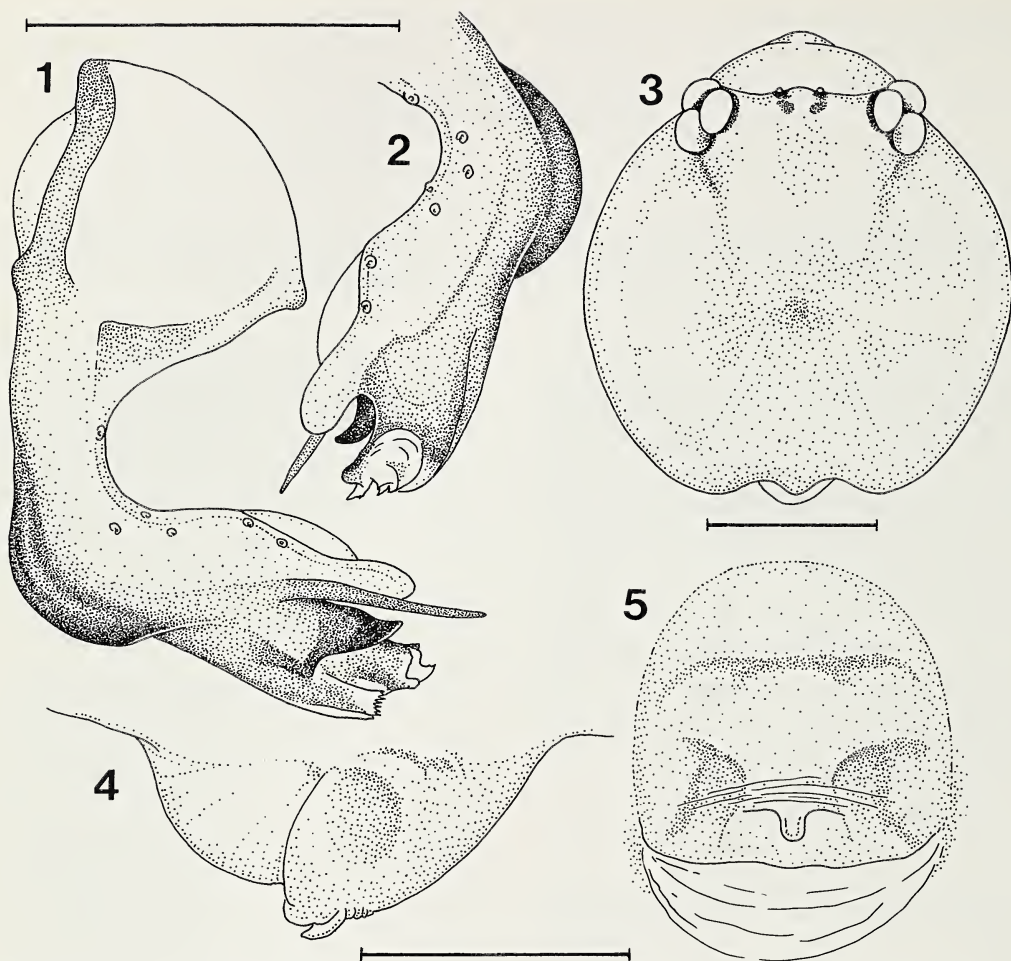
Figures 1–5.—*Leptopholcus delicatulus* Franganillo 1930, diagnostic characters. 1, Left cymbium with procursus, prolateral view; 2, Left procursus, retrolateral view; 3, Female prosoma, dorsal view; 4, Epigynum, lateral view; 5, Epigynum, ventral view. Scale bars = 0.3 mm.

characters and on measurements of type and non-type material.

Male chelicerae with two pairs of apophyses (Fig. 11). Genital bulb with prominent apophysis accompanying the embolus (Fig. 12). Tip of procursus with a complex system of projections (Figs. 13, 14). Pedipalpal tarsal organs as shown in Figs. 15 (female) and 16 (male). Epigynum as in Fig. 17. Male genital opening with four epiandrous spigots (Fig. 18). Anterior median spinnerets with several spigots (Fig. 19), posterior median spinnerets with a single pair of spigots each (Fig. 20) (there was no obvious sexual dimorphism in the spinnerets).

Measurements of female lectotype (mm): prosoma width: 0.8, prosoma length: 0.8,

opisthosoma length: 3.5; legs (Total—Fem, Pat, Tib, Met, Tar): I (23.1—5.8, 0.3, 5.4, 9.9, 1.7), II (14.7—4.2, 0.3, 3.5, 5.8, 0.9), III (9.7—3.0, 0.3, 2.2, 3.5, 0.7), IV (15.7—4.9, 0.3, 3.7, 5.9, 0.9). Measurements of a male from Sierra de San Carlos (mm): prosoma width: 0.9, prosoma length: 0.9, opisthosoma length: 3.9; legs (Total—Fem, Pat, Tib, Met, Tar): I (33.3—8.1, 0.4, 8.0, 14.8, 2.0), II (21.4—5.7, 0.4, 5.5, 8.8, 1.0), III (13.8—4.1, 0.4, 3.4, 5.2, 0.7), IV (20.9—6.2, 0.4, 5.2, 8.2, 0.9). Tibia 1 length in other material (mm): 8♂: 6.0–7.5 ($\bar{x}$ = 6.9); 16♀: 4.9–6.3 ($\bar{x}$ = 5.7).

Distribution.—Figure 21 suggests that *L. delicatulus* has a wide distribution in Cuba. The same is true for *L. dalei* in Puerto Rico.
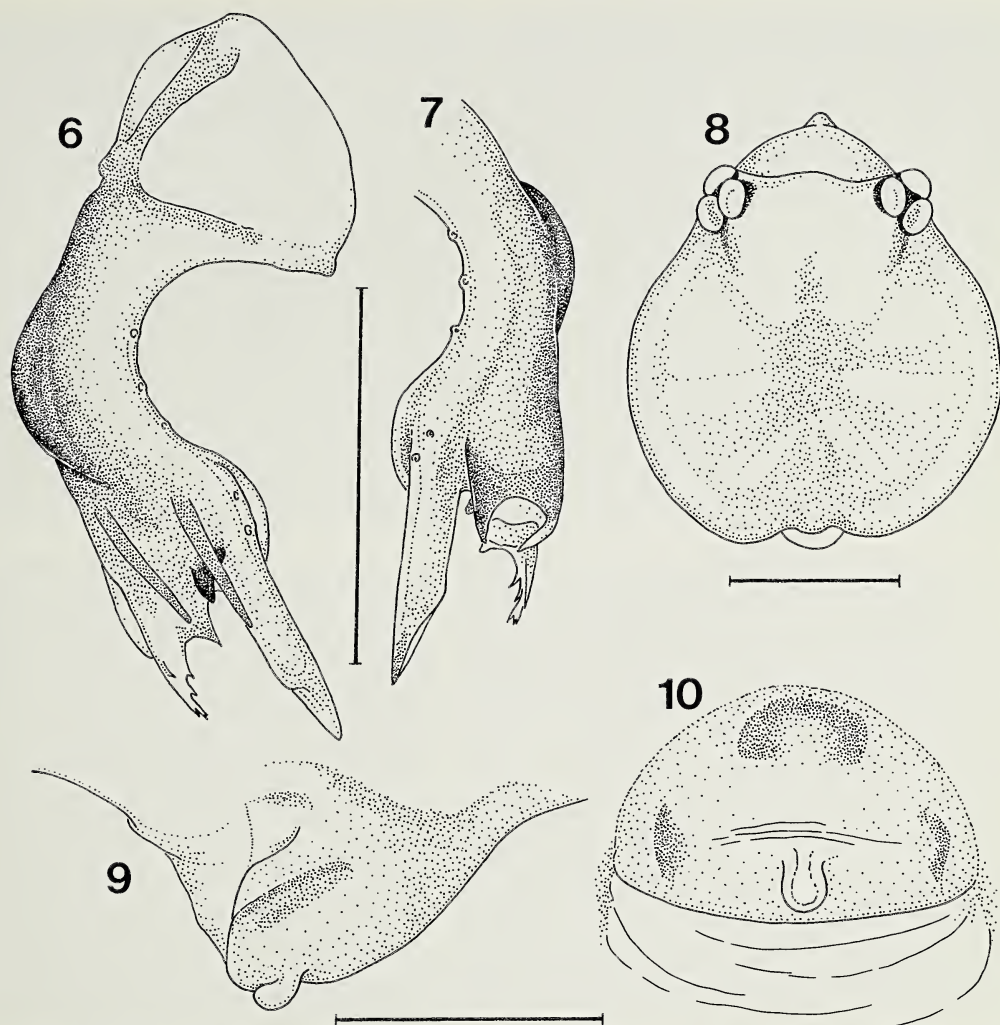
Figures 6–10.—*Leptopholcus dalei* (Petrunkevitch 1929), diagnostic characters. 6, Left cymbium with procursus, prolateral view; 7, Left procursus, retrolateral view; 8, Female prosoma, dorsal view; 9, Epigynum, lateral view; 10, Epigynum, ventral view. Scale bars = 0.3 mm.

However, neither species nor any other *Leptopholcus* has so far been recorded from any of the nearby islands.

Material examined.—(IES: Instituto de Ecología y Sistematica, La Habana, Cuba; ColKarst: collection of BioKarst of the Sociedad Espeleológica de Cuba; AMNH: American Museum of Natural History, New York): **CUBA:** *Prov. Pinar del Río:* ♀ lectotype and 5♀ paralectotypes from Cordillera de Guaniguanico (no collection data) (collection P. Franganillo, #208, IES). 1♂ from Sierra de San Carlos, Mogote de la cueva La Viñalera, 9 March 1994 (A. Pérez González) (IES). 1♂1♀ from Sierra de San Carlos, Hoyo de los Helechos, 16 February 1991 (A. Pérez González) (IES). 4♀ from entrance to Las Dos Anas cave, Majaguas-Cantera cave system, Sierra de San Carlos, 17 March 1991 (A. Pérez González) (ColKarst). 1♀ from Mogote el Moncada, 14 March 1976 (R. Rodríguez Soberón). *Prov. Habana:* 1♂ from the bank of the Cojimar River, Cojimar, Ciudad de La Habana, Cuba, 26 June 1996 (A. Pérez González) (IES). *Prov. Sancti Spiritus:* 1♀ from 1 km N Batey del Medio, Meneses, Cuba, May 1978 (L.F. de Armas). *Prov. Guantánamo:* 6♂6♀ from Vazquez, Riito, National Park Alejandro de Humboldt, 10 February 1997 (A. Pérez González), 1♂1♀ deposited in AMNH, rest in IES. 1♀ from El Poal, Jaguaní River, National Park Alejandro de Humboldt, 10 August 1992 (A. Pérez González), in coll. B.A. Huber; 2♂3♀ from same lo-
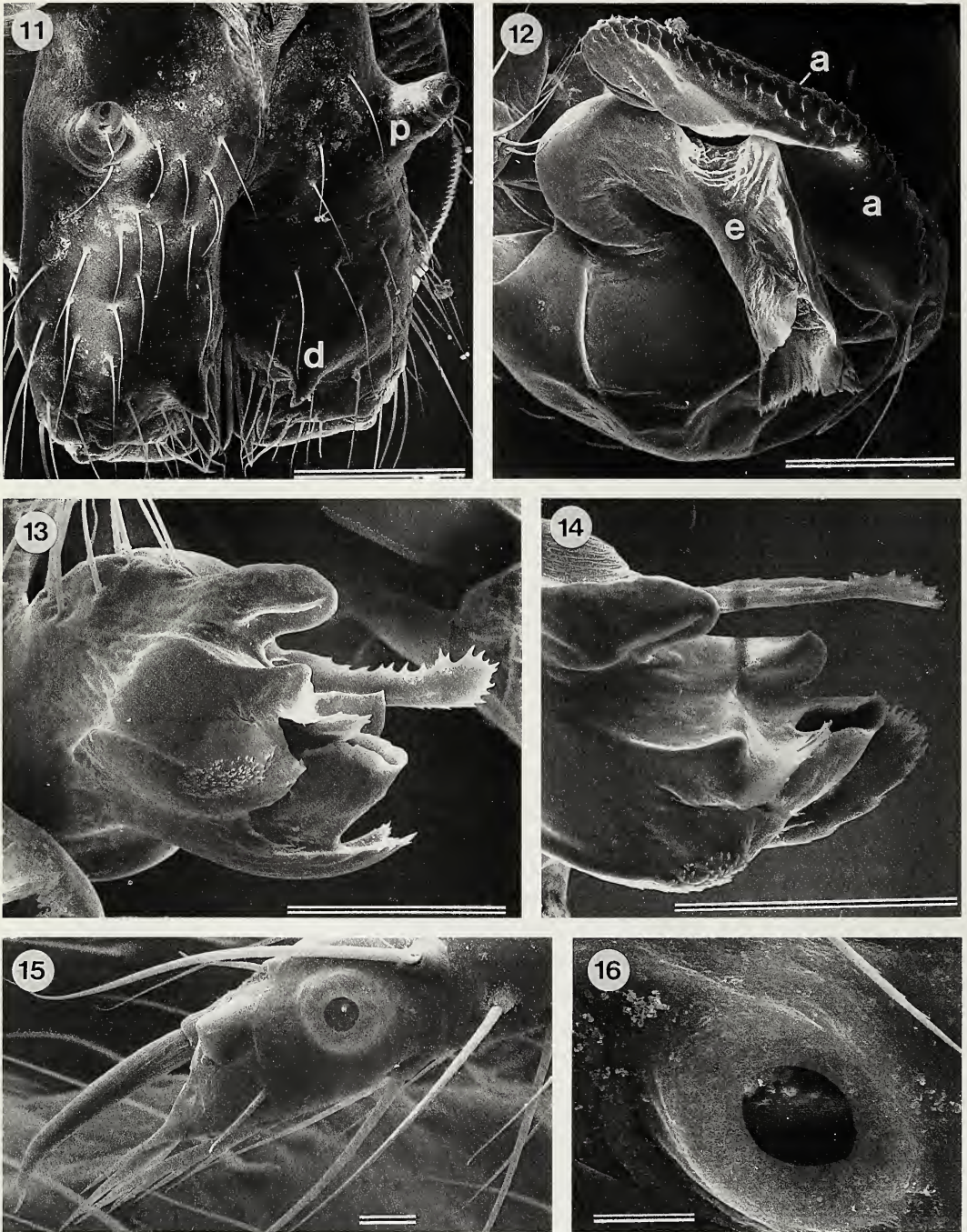
Figures 11–16.—*Leptopholcus delicatulus* Franganillo 1930. 11, Male chelicerae, showing proximal (p) and distal (d) apophyses; 12, Genital bulb, with embolus (e) and accompanying apophysis (a); 13, 14, Tip of procursus, approximately retrolateral view; 15, Tip of female pedipalp with tarsal organ; 16, Male pedipalpal tarsal organ. Scale bars = 0.1 mm (11–14); 0.01 mm (15, 16).
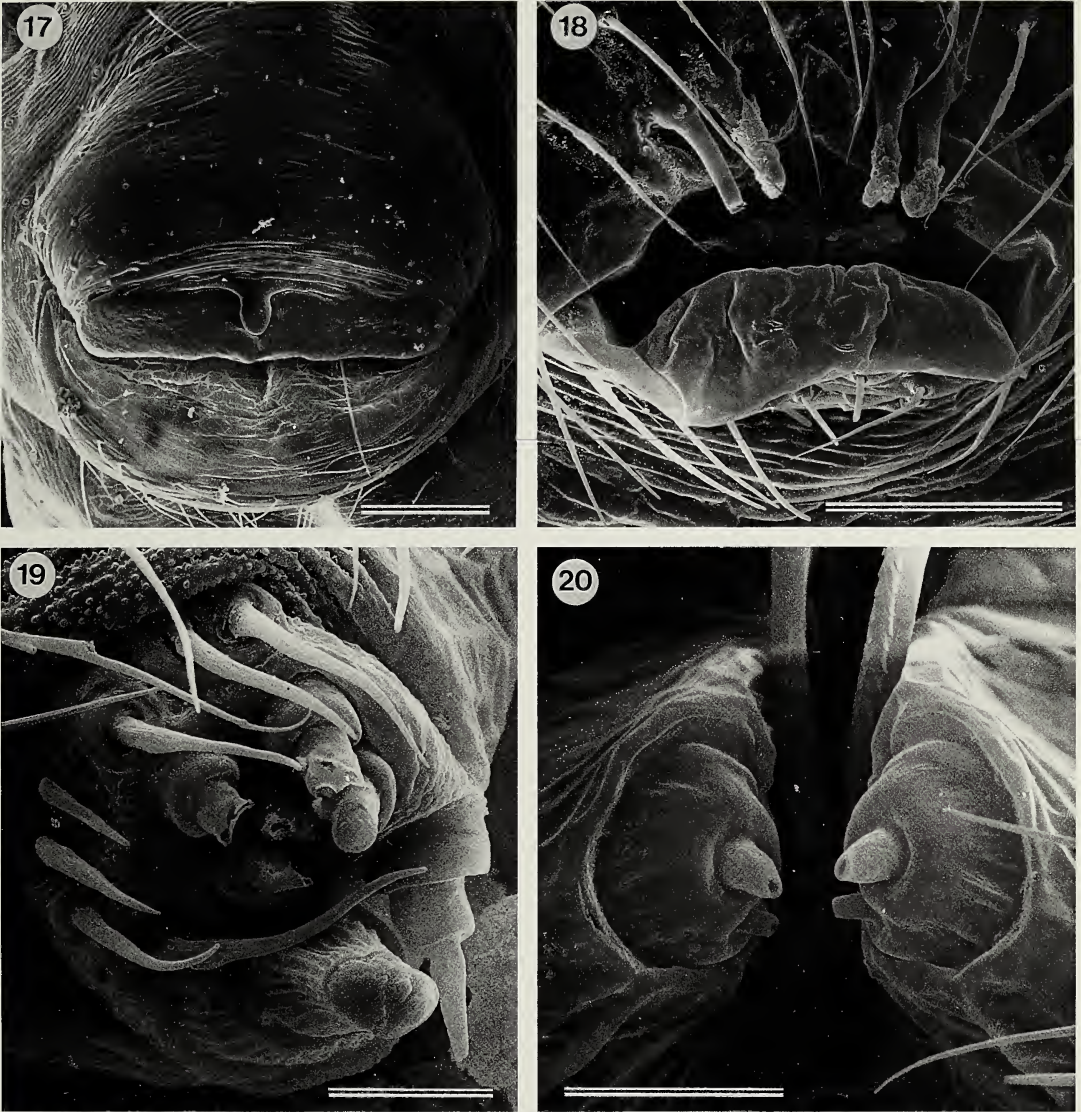
Figures 17–20.—*Leptopholcus delicatulus* Franganillo 1930. 17, Epigynum, ventral view; 18, Male genital opening with epiandrous spigots; 19, Female right anterior spinneret; 20, Female posterior median spinnerets. Scale bars = 0.1 mm (17); 0.05 mm (18); 0.01 mm (19, 20).

cality, 8, 11 & 16 August 1992 (A. Pérez González, M. Estrada) (IES).

Natural history.—The present species is apparently restricted to humid forests, and seems to prefer glens to crests. It has been collected at elevations ranging from sea level (Cojimar) to about 1500 m (Pico Turquino—Bryant 1940). During the day the apparently nightactive spiders sit on the underside of leaves, pressing their body against the surface and extending the legs.

Discussion.—Bryant (1940) synonymized the two Cuban species with the Puerto Rican *L. dalei* Petrunkevitch 1929. Her own Cuban material could not be found at the Museum of Comparative Zoology, and might therefore be lost. We consider it *L. delicatulus* primarily because of the presence of anterior median eyes (Bryant 1940). Bryant decided on the synonymy after comparing her specimens with Petrunkevitch's (1929) drawings. Though these drawings are good, they do not show sufficient detail of the procursus, which is evidently the reason for Bryant's error.

Figure 21.—Geographic distribution of the two known American *Leptopholcus* species. The localities included are those from the present paper, Franganillo (1930, 1931), and Bryant (1940) for *L. delicatulus,* and those from Petrunkevitch (1929) and Huber (1997) for *L. dalei.*

Leptopholcus dalei has been redescribed recently in order to clarify its distant relationship with American "Micromerys" and *Metagonia* (Huber 1997). As stated in that paper for *L. dalei,* the generic position of *L. delicatulus* is beyond the scope of the present note. In fact, judging by the male bulb, African *Leptopholcus* appear closer to *Pholcus* than to the two American *Leptopholcus* species (cf. Brignoli 1980; Uhl et al. 1995; Huber 1997; and this note).

ACKNOWLEDGMENTS

LITERATURE CITED

Brignoli, P.M. 1980. Sur le genre *Leptopholcus* Simon, 1893 (Araneae, Pholcidae). Rev. Zool. Afrique, 93:649–655.

Bryant, E.B. 1940. Cuban spiders in the Museum of Comparative Zoology. Bull. Mus. Comp. Zool., 86:247–532.

Franganillo B., P. 1930. Aracnidos de Cuba. Más arácnidos de la Isla de Cuba. Mem. Inst. Nacional de Invest. Cient., 1:47–97.

Franganillo B., P. 1931. Excursiones aracnológicas, durante el mes de agosto de 1930. Revista "Belen", La Habana, 27–28:285–288.

Franganillo B., P. 1934. Arácnidos Cubanos estu-

diados deste 1930 hasta 1934. Mem. Soc. Cubana Hist. Natur., 8:145–168.

Franganillo B., P. 1936a. Los Arácnidos de Cuba hasta 1936. Cultural, S.A., La Habana, Cuba (1936):45–47.

Franganillo B., P. 1936b. Arácnidos recogidos durante el verano de 1934. Revista "Belen", La Habana (1936):75–78.

Huber, B.A. 1997. On American 'Micromerys' and *Metagonia* (Araneae, Pholcidae), with notes on natural history and genital mechanics. Zool. Scripta, 25:341–363.

Huber, B.A. & W.G. Eberhard. 1997. Courtship, copulation and genital mechanics in *Physocyclus globosus* (Araneae, Pholcidae). Canadian J. Zool., 74:905–918.

Petrunkevitch, A. 1929. The spiders of Porto Rico. Trans. Connecticut Acad. Arts Sci., 30:1–158.

Uhl, G., B.A. Huber, & W. Rose. 1995. Male pedipalp morphology and copulatory mechanism in *Pholcus phalangioides* (Fuesslin, 1775) (Araneae, Pholcidae). Bull. British Arachnol. Soc., 10: 1–9.

[1] **Bernhard A. Huber**:   Escuela de Biología, Universidad de Costa Rica, Costa Rica

Abel Pérez González: Instituto de Ecología y Sistematica, Habana 8, Cuba

[1]*Current address:* Dept. of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, N.Y. 10024 USA

INSTRUCTIONS TO AUTHORS
(revised October 1996)

Manuscripts are preferred in English but may be accepted in Spanish, French or Portuguese subject to availability of appropriate reviewers. Authors whose primary language is not English may consult the Associate Editor for assistance in obtaining help with English manuscript preparation. All manuscripts should be prepared in general accordance with the current edition of the *Council of Biological Editors Style Manual* unless instructed otherwise below. Authors are advised to consult a recent issue of the *Journal of Arachnology* for additional points of style. Manuscripts longer than 1500 words should be prepared as Feature Articles, shorter papers as Research Notes. Send **four** identical copies of the typed material together with photocopies of illustrations to the **Managing Editor**. Do not send original handmade illustrations until the manuscript has been accepted. Mail to:

Petra Sierwald, Managing Editor; Division of Insects, Dept. of Zoology, Field Museum, Roosevelt Road at Lakeshore Drive, Chicago, IL 60605 USA [Telephone: (312) 922-9410, ext. 841; FAX: (312) 663-5397; E-mail: SIERWALD@FMNH.ORG]

Correspondence relating to the initial submission of a manuscript, as well as the review process, should be directed to the Associate Editor. Correspondence relating all other matters should be directed to the Editor. After the manuscript has been accepted, the author will be asked to submit the manuscript on a computer disc. It must be in a widely used program (preferably in MS DOS WordPerfect). Indicate clearly on the computer disc the word processing program used.

FEATURE ARTICLES

Title page.—The title page will include the complete name, address, and telephone number of the author with whom proofs and correspondence should be exchanged, a FAX number and electronic mail address if available, the title in capital letters, and each author's name and address, and the running head (see below).

Abstract.—The heading in capital letters should be placed at the beginning of the first paragraph set off by a period. In articles written in English, a second abstract in an acceptable language may be included pertinent to the nationality of the author(s) or geographic region(s) emphasized in the article. A second abstract in English must be included in articles not written in the latter language.

Text.—Double-space text, tables, legends, etc. throughout. Three levels of heads are used. The first level (METHODS, RESULTS, etc.) is typed in capitals and on a separate line. The second level head begins a paragraph with an indent and is separated from the text by a period and a dash. The third level may or may not begin a paragraph but is italicized and separated from the text by a colon. Use only the metric system unless quoting text or referencing collection data. All decimal fractions are indicated by the period regardless of language of the text.

Citation of references in the text: Cite only papers already published or in press. Include within parentheses the surname of the author followed by the date of publication. A comma separates multiple citations by the same author(s) and a semicolon separates citations by different authors, e.g., (Smith 1970), (Jones 1988; Smith 1993), (Smith 1986, 1987; Smith & Jones 1989; Jones et al. 1990).

Literature cited section.—Use the following style:

Lombardi, S. J. & D. L. Kaplan. 1990. The amino acid composition of major ampullate gland silk (dragline) of *Nephila clavipes* (Araneae, Tetragnathidae). J. Arachnol., 18:297–306.
Krafft, B. 1982. The significance and complexity of communication in spiders. Pp. 15–66, *In* Spider

Communications: Mechanisms and Ecological Significance. (P. N. Witt & J. S. Rovner, eds.). Princeton University Press, Princeton, New Jersey.

Footnotes.—Footnotes are permitted only on the first printed page to indicate current address or other information concerning the author. All footnotes are placed together on a separate manuscript page.

Running head.—The author surname(s) and an abbreviated title should be typed all in capital letters and must not exceed 60 characters and spaces. The running head should be placed near the top of the title page.

Taxonomic articles.—Consult a recent taxonomic article in the *Journal of Arachnology* for style or contact the Editor.

Tables.—Each table, with the legend above, should be placed on a separate manuscript page. Only horizontal lines (usually three) should be included. Use no footnotes; instead, include all information in the legend. Make notations in the text margins to indicate the preferred location of tables in the printed text.

Illustrations.—Address all questions concerning illustrations to:

James W. Berry, Editor; Dept. of Biological Sciences, Butler University, Indianapolis, Indiana 46208 USA [Telephone (317) 940-9344; FAX (317) 940-9519; E-mail: jwberry@thomas.butler.edu]

All art work must be camera-ready for reproduction. In line drawings, pay particular attention to width of lines and size of lettering when reductions are to be made by the printer. Multiple photos assembled on a single plate should be mounted with only a minimum of space separating them. In the case of multiple illustrations mounted together, each illustration must be numbered sequentially rather than given an alphabetic sequence. Written on the back should be the name(s) of author(s) and an indication of top edge. The author should indicate whether the illustrations should be one column or two columns in width. The overall dimensions of original artwork should be no more than 11 inches (28 cm) × 14 inches (36 cm). Photocopies in review manuscripts should be reduced to the exact measurements that the author wants to appear in the final publication. Larger drawings present greater difficulty in shipping and greater risks of damage for which the JOA assumes no responsibility. Make notations in the text margins to indicate the preferred position of illustrations in the printed text.

Legends for illustrations should be placed together on the same page(s) and separate from the illustrations. Each plate must have only one legend, as indicated below:

Figures 1–4.—*A-us x-us,* male from Timbuktu. 1, Left leg; 2, Right chelicera; 3, Dorsal aspect of genitalia; 4, Ventral aspect of abdomen.

Figures 27–34.—Right chelicerae of species of *A-us* from Timbuktu. 27, 29, 31, 33, Dorsal views; 28, 30, 32, 34, Prolateral views of moveable finger; 27, 28, *A-us x-us,* holotype male; 33, 34, *A-us y-us,* male. Scale = 1.0 mm.

Assemble manuscript for mailing.—Assemble the separate sections or pages in the following sequence: title page, abstract, text, figure legends, footnotes, tables with legends, figures.

Page charges, proofs and reprints.—There are no page charges, but authors will be charged for changes made in the proof pages. Authors will receive a reprint order form along with their page proofs. Reprints will be billed at the printer's current schedule of costs.

RESEARCH NOTES

Instructions above pertaining to feature articles apply also to research notes, except that abstracts and most headings are not used and the author's name and address follow the Literature Cited section.
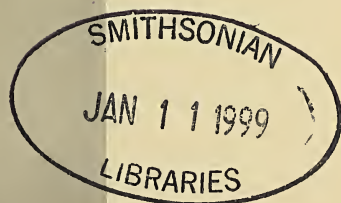
CONTENTS

The Journal of Arachnology

The Journal of
ARACHNOLOGY

JOSEPH C. CHAMBERLIN
(1898-1962)

THE JOURNAL OF ARACHNOLOGY

THE AMERICAN ARACHNOLOGICAL SOCIETY

Cover photo: As a tribute to the arachnologist, Joseph C. Chamberlin, a series of papers on pseudoscorpions is included in this issue—on the 100th anniversary of his birth, 23 December 1898.

Publication date: 23 December 1998

⊗ This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).

PHYLOGENY OF OPILIONES (ARACHNIDA): AN ASSESSMENT OF THE "CYPHOPALPATORES" CONCEPT

Jeffrey W. Shultz: Department of Entomology, University of Maryland, College Park, Maryland 20742-4454 USA

ABSTRACT. The arachnid order Opiliones has typically been divided into three suborders (Cyphophthalmi, Laniatores and Palpatores), but this system has been challenged in recent years. Based on scenarios of genitalic evolution, Martens and coworkers have argued that certain lineages within Palpatores are more closely related to Cyphophthalmi than to other palpatorean opilions and erected a new clade, Cyphopalpatores, to accommodate this proposal. However, this system is also problematic. Because most genitalic characters within Opiliones are unique to that order, genitalic characters cannot be polarized and opilion phylogeny cannot be rooted using objective outgroup comparison. Thus the Cyphopalpatores concept rests heavily on speculative scenarios of character evolution. The goal of the present study was to examine relationships among the major lineages of Opiliones using both genitalic and non-genitalic characters and thereby assess the Cyphopalpatores concept and associated scenarios of genitalic evolution. Maximum-parsimony analysis of a matrix composed of 17 terminal taxa (including two outgroups) and 26 binary and multistate characters recovered a minimal-length topology that was incompatible with the Cyphopalpatores concept but suggested that Cyphophthalmi is the sister group to a clade comprising a monophyletic Palpatores and monophyletic Laniatores. In contrast, the most-parsimonious distribution of characters within the minimal-length topology supported many of the character transformation series upon which the Cyphopalpatores concept was based. This result reaffirms the observation that a given hypothesis of character evolution can be consistent with several phylogenetic hypotheses and that an empirically robust phylogenetic analysis should include more than one character system.

For the last two decades, discussions of higher-level relationships within Opiliones have been heavily influenced by the phylogenetic hypotheses proposed by Martens and his coworkers (Martens 1976, 1980, 1986; Hoheisel 1980; Martens, Hoheisel & Götze 1981). Prior to these hypotheses, Opiliones had generally been divided into three principal clades, namely, Cyphophthalmi, Palpatores and Laniatores (Hansen & Sörensen 1904; Roewer 1923; Shear 1982; Hennig 1986; see Šilhavý 1961 for an alternative). However, based primarily on analysis of selected genitalic characters, Martens and coworkers argued that Palpatores is paraphyletic. Specifically, they proposed that the palpatorean superfamily Troguloidea is the sister group to a clade comprising Cyphophthalmi and the palpatorean superfamilies Phalangioidea, Caddoidea and Ischyropsalidoidea (Fig. 1) and erected a new clade (Cyphopalpatores) to accommodate the non-laniatorean opilions. Although the Cyphopalpatores concept has yet to undergo explicit numerical assessment, it was accepted by some opilionologists and influenced family- and genus-level revisions

within Troguloidea (Shear & Gruber 1983) and Ischyropsalidoidea (Shear 1986) (Fig. 2). The goal of the present study was to assess the Cyphopalpatores hypothesis by conducting maximum-parsimony analysis on representative opilions using genitalic and non-genitalic characters.

Several aspects of the original formulation of the Cyphopalpatores concept are open to question and must be considered when devising fair and appropriate tests of the hypothesis. First, Martens and coworkers based their conclusions on a small fraction of the taxonomic diversity known to exist within Opiliones (i.e., 21 out of more than 4500 species). Such an approach is valid and expected when data are derived from intensive morphology-based analyses, but the resulting data are strictly applicable only to resolving relationships among those terminal taxa actually observed. However, Martens and coworkers used their results to address relationships among eight superfamilies (i.e., Sironoidea, Travunioidea, Gonyleptoidea, Oncopodoidea, Phalangioidea, Caddoidea, Ischyropsalidoidea, Troguloidea) without demonstrating the mono-
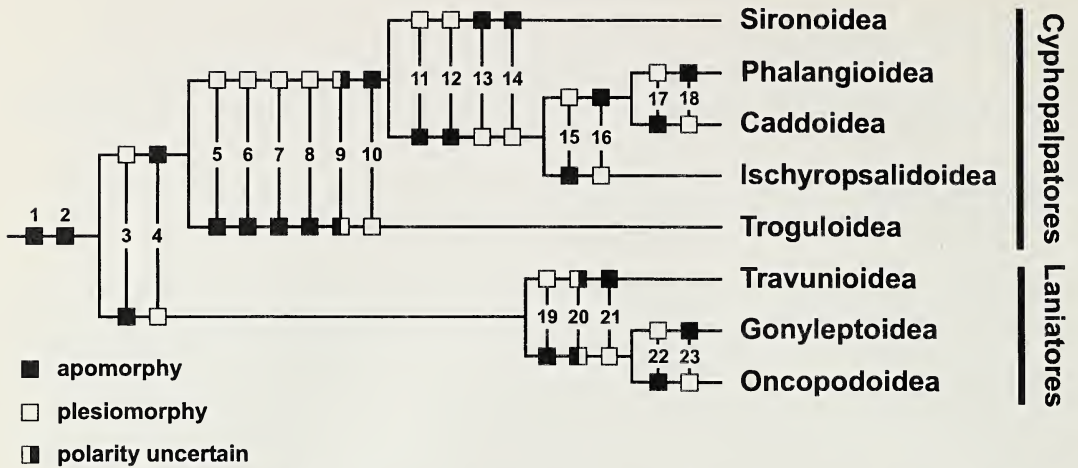
Figure 1.—Phylogeny of the superfamilies in Opiliones proposed by Martens (1980, 1986) and Martens et al. (1981). The first state of each character is the apomorphic state; the state in parentheses is the plesiomorphic state. 1, ovipositor; 2, penis; 3, x-shaped vagina present (absent), 4, ovipositor with segmentally arranged chitinous rings (ovipositor primitively unsegmented); 5, two penis muscles (three penis muscles); 6, ovipositor secondarily unsegmented (ovipositor with segmentally arranged chitinous rings); 7, sternum fused to leg coxae (not fused to leg coxae); 8, pedipalpal setae clavate, glandular (setae unspecialized); 9, outer circular muscles present in ovipositor (outer ring muscles absent); 10, colleterial glands of ovipositor compact, drained by large duct (glands aciniform, drained by many small ducts); 11, penis with one median muscle (three muscles); 12, pedipalpal setae plumose (pedipalpal setae not plumose); 13, genital operculum not covering genital opening (operculum covering genital opening); 14, tendency toward scutum completum (no such tendency); 15, ovipositor secondarily unsegmented (ovipositor with segmentally arranged chitinous rings); 16, inner surface of ovipositor sheath lined with cuticular hooks (not lined with cuticular hooks); 17, tendency toward reduction in number of chitinous rings in ovipositor (no such tendency); 18, leg tibia with accessory tracheal stigmata (no accessory stigmata); 19, median penis muscle reduced (one median longitudinal muscle); 20, ovipositor with 4 lobes (2 lobes); 21, ovipositor with inner longitudinal muscle (without inner longitudinal muscle); 22, tendency toward fusion of tergites into scutum completum (no such tendency); 23, cells of colleterial glands consolidated into a few functional units and concentrated in terminal lobes of the ovipositor (many functional units formed from small cells and distributed in the vaginal epithelium).

phyly of each superfamily or that the assigned states were synapomorphic for each superfamily as a whole. Second, Martens and coworkers chose to resolve opilion phylogeny using a character system unique to Opiliones, and thereby virtually eliminated the possibility of assigning character polarity or of rooting their phylogeny by objective reference to outgroups. Rather than offer an unrooted phylogenetic network, Martens and coworkers relied on speculative scenarios of genitalic evolution to polarize characters and to root their tree. Finally, comparisons of the character descriptions, tabulations and phylogenetic tree presented in Martens et al. (1981) revealed that these workers did not include all relevant genitalic characters in their analysis but offered no justification for their selection.

Based on these observations, the Cypho-

palpatores concept was assessed in the following way. First, the taxon sample was essentially identical at the generic level to that used by Martens et al. (1981), and genera rather than superfamilies were used as terminal taxa. This approach ensured that differences between the results of Martens et al. and the present study would not be due to differences in taxon representation and also avoided problems associated with assigning "synthetic" character states to higher-level taxa of doubtful monophyly. Second, opilion phylogeny was rooted by including outgroups and variable somatic (non-genitalic) characters expressed in both Opiliones and the outgroups. To avoid the circularity inherent in basing phylogeny on preconceived notions of character evolution, polarities were inferred in the course of computerized maximum-parsimony
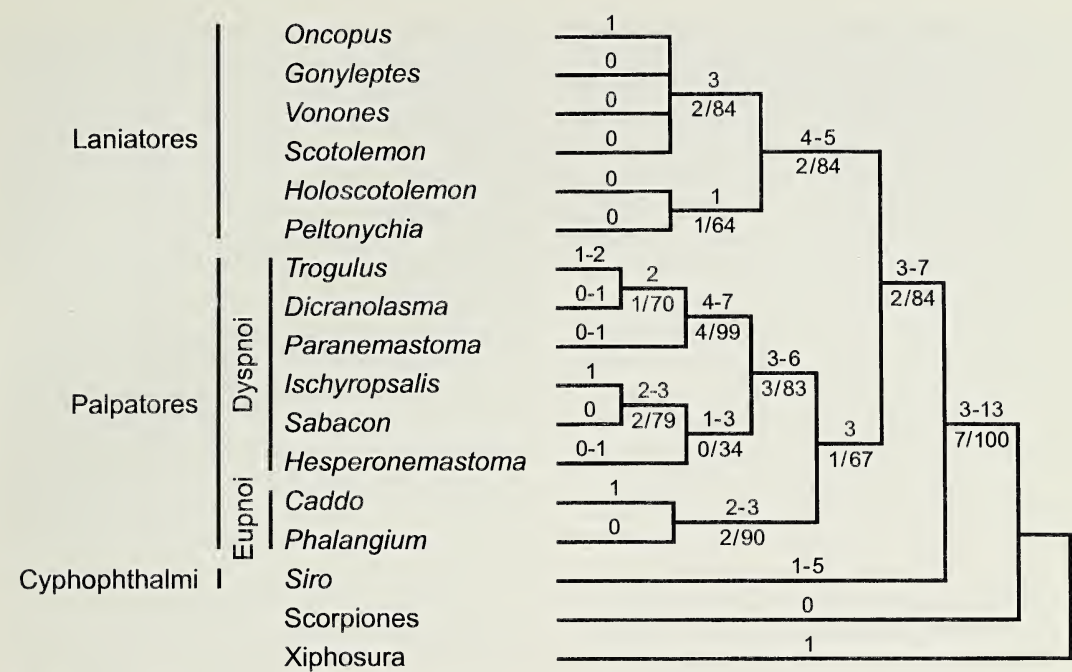
Figure 2.—One of two minimal-length topologies constructed for Opiliones using the data matrix in Table 1. In the other topology, *Hesperonemastoma* is reconstructed as the sister group to ((*Ischyropsalis, Sabacon*),(*Paranemastoma*, (*Dicranolasma, Trogulus*))). Numbers above branches represent minimum-to-maximum branch length; numbers below branches represent decay index/bootstrap percentage. The tree depicted here is the only minimal-length topology found under successive weighting using consistency and retention indices.

analysis. Finally, biases resulting from subjective character selection were minimized by including 11 relevant genitalic characters presented by Martens et al. (1981).

The results derived from this approach were inconsistent with the Cyphopalpatores concept and suggested that Cyphophthalmi (= Superfamily Sironoidea) is the sister group to a clade comprising Palpatores (superfamilies Phalangioidea, Caddoidea, Ischyropsalidoidea, Troguloidea) and Laniatores (superfamilies Travunioidea, Gonyleptoidea, Oncopodoidea). This phylogeny has been a predecessor and principal alternative to the Cyphopalpatores concept (e.g., Juberthie & Manier 1978; Hennig 1986). Furthermore, Palpatores is reconstructed as being composed of two clades that correspond broadly to the Eupnoi/Dyspnoi dichotomy originally framed by Hansen & Sörensen (1904). Despite the poor performance of the Cyphopalpatores concept as a phylogenetic hypothesis, the pathways of character evolution suggested by the present analysis were consistent with several of the

character transformation series upon which the Cyphopalpatores concept was based. This inconsistency suggests that systematists who favor the qualitative, scenario-based approach to cladistic analysis over quantitative, parsimony-based approaches should consider that any given evolutionary scenario may be consistent with multiple phylogenetic hypotheses and that an assessment of phylogenetic signal within other characters is essential for reaching evolutionary conclusions that are empirically robust and free from circular reasoning.

METHODS

Terminal taxa.—*Outgroups:* Phylogenetic relationships among arachnid orders are controversial. Opiliones has often been placed near Acari and/or Ricinulei (e.g., Savory 1971; Yoshikura 1975), a hypothesis supported by Weygoldt & Paulus (1979) in an influential study of chelicerate phylogeny. In contrast, Shultz (1990) conducted a morphology-based parsimony analysis which suggested that Opiliones is an early divergent mem-

ber of Arachnida and is the sister group to a clade encompassing Scorpiones, Pseudoscorpiones and Solifugae. Several arachnologists have questioned this hypothesis (e.g., Selden 1990), but no evidence or analysis has been put forward to refute the proposed placement of Opiliones. Consequently, based on Shultz's proposal that Opiliones is an early divergent group of arachnids, Xiphosura and Scorpiones were selected as outgroups.

Ingroups: Opiliones is clearly monophyletic and united by many apomorphic characters, including an ovipositor, spermatopositor/penis, nine complete opisthosomal somites, a single pair of sternal tracheal stigmata, and prosomal glands opening on the carapace via ozopores. The order is here represented by 15 terminal taxa, which are discussed briefly below.

Superfamily Sironoidea: The sironoids are small, heavily sclerotized opilions characterized by many autapomorphies (e.g., elevated ozopores, unique coxosternal arrangement, male adenostyles) (Shear 1980, 1982), and the monophyly of the superfamily is unquestioned. The distinctiveness of sironoids has led them to be placed in their own suborder, Cyphophthalmi (Hansen & Sörensen 1904). Sironoidea is here represented by *Siro* Latreille 1796. Martens et al. (1981) based their characterization of the sironoid ovipositor on original observations of two species, *Siro duricorius* (Joseph 1868) and *S. rubens* (Latreille 1804), but Martens (1986) synthesized information from many species to obtain character states for the male genitalia. Somatic characters used in the present study were based on *Siro acaroides* (Ewing 1923) and other *Siro* species obtained from the literature and from original observations.

Superfamily Travunioidea: This superfamily comprises several families of laniatorean opilions distributed mainly in temperate regions in the northern and southern hemispheres. The travunioids are typically defined as laniatorean opilions with a muscularized penis, a character that may be primitive, and the group may be paraphyletic with respect to gonyleptoids and oncopodoids. The travunioids are represented in the present analysis by two genera, *Peltonychia* (Travuniidae) and *Holoscotolemon* Roewer 1915 (Cladonychiidae). Martens et al. (1981) examined the ovipositors of *Peltonychia clavigera* (Simon 1872), *Holoscotolemon unicolor* Roewer 1915 and *Theromaster brunnea* (Banks 1902) (Cladonychiidae). They found few differences between *Holoscotolemon* and *Theromaster,* none of which were important for purposes of the present study. Martens (1986) depicted the penes of a *Peltonychia* species and *H. unicolor.* Somatic characters for the two genera were obtained from the literature and original observations.

Superfamily Gonyleptoidea: The gonyleptoids are a morphologically diverse and species-rich assemblage of 18 or so families that range throughout most temperate and tropical regions but are especially diverse in the tropics. More families may be recognized as genitalic diversity within the group becomes better known (Martens 1988). There appears to be no well-documented synapomorphies for the superfamily. Shear (1982) noted that gonyleptoids have a penis that lacks intrinsic longitudinal muscles as well as paired claws on the posterior legs, but both traits are also present in Oncopodoidea (Roewer 1923; Martens 1986). Consequently, it is possible that Gonyleptoidea is paraphyletic with respect to oncopodoids. The gonyleptoids are represented here by three genera, *Scotolemon* Lucas 1860 (Phalangodidae), *Vonones* Simon 1879 (Cosmetidae) and *Gonyleptes* Kirby 1819 (Gonyleptidae). Martens et al. (1981) based their model of the gonyleptoid ovipositor on original observations of *Bishopella laciniosa* (Crosby & Bishop 1924) (Phalangodidae), *Scotolemon lespesi* Lucas 1860, *Vonones sayi* (Simon 1879) and an unspecified gonyleptid. There were no substantial differences between the ovipositors of *Bishopella* and *Scotolemon,* so the former was omitted from the present analysis. Somatic and male genitalic characters were determined for *Scotolemon lespesi, Vonones ornata* (Say 1921) and *Gonyleptes* spp. from the literature and from original observations.

Superfamily Oncopodoidea: The oncopodoids encompass several genera from southeastern Asia. They generally resemble gonyleptoids but are distinguished by a suite of autapomorphies (Roewer 1923; Shear 1982). The superfamily is represented here by the genus *Oncopus* Thorell 1876. Martens et al. (1981) examined the ovipositor of *Oncopus acanthochelis* Roewer 1915, and Martens (1986) based his model of the oncopodoid pe-

nis on examination of *Oncopus* and *Pelitnus* Thorell 1891. Somatic characters were obtained from the literature.

Superfamily Phalangioidea: This species-rich superfamily encompasses several, often poorly delimited families with representatives present on all continents except Antarctica. Phalangioids are frequently united on the basis of a single synapomorphy, the presence of tibial spiracles. The superfamily is here represented by *Phalangium* Linneus 1758 (Phalangiidae). Martens et al. (1981) examined the ovipositor in the phalangiids *P. opilio* Linneus 1761, three species of *Opilio* Herbst 1778, and *Lacinius ephippiatus* (C.L. Koch 1835). There were no substantial differences among these taxa. Phalangioid penial characters were obtained from Martens (1986). Somatic characters were derived from the literature and original observations of *P. opilio.*

Superfamily Caddoidea: The superfamily includes several genera from North America, southern South America, New Zealand, Australia, Japan and South Africa. They resemble small phalangioids but differ in having large eye tubercles and apparently raptorial pedipalps (Shear 1982). Several workers recognize two caddoid families, Caddidae and Acropsopilionidae (e.g., Cokendolpher & Maury 1990), but others advocate only one, Caddidae (e.g., Shear 1996). The superfamily is here represented by *Caddo* Banks 1892. Martens et al. (1981) based their character analysis of the caddoid ovipositor on one species, *Caddo agilis* (Banks 1892), although substantial variation in ovipositor structure is known to exist in the superfamily (Gruber 1974; Shear 1996). Likewise, Martens (1986) apparently used the penis of *C. agilis* (Gruber 1974) as representative, although the penis also shows considerable variation in the superfamily (e.g., Shear 1996). Somatic characters used in the present analysis were obtained from the literature and from original observations of *C. agilis* and *C. pepperella* Shear 1975.

Superfamily Ischyropsalidoidea: The superfamily encompasses at least seven genera, namely, *Ischyropsalis* C.L. Koch 1839, *Sabacon* Simon 1879, *Taracus* Simon 1879, *Acuclavella* Shear 1986, *Ceratolasma* Goodnight & Goodnight 1942, *Hesperonemastoma* Gruber 1970 and *Crosbycus* (Crosby 1911), with a generally Holarctic distribution. The phylogenetic and taxonomic structure within the su-

perfamily is controversial and has been treated most recently by Shear (1986). Following Martens et al. (1981), Ischyropsalidoidea is represented here by *Ischyropsalis, Sabacon* and *Hesperonemastoma.* Martens et al. derived their model of the ischyropsalidoid ovipositor from original examinations of *Ischyropsalis luteipes* Simon 1879, *Sabacon viscayanum* Simon 1881 and *Hesperonemastoma kepharti* (Crosby & Bishop 1924). Ischyropsalidoid penial characters were obtained from Martens (1986). Somatic characters are based on observations of *Ischyropsalis luteipes, I. hellwigi* (Panzer 1796), *Sabacon cavicolens* (Packard 1884) and *Hesperonemastoma modestum* (Banks 1894) obtained from the literature and from original observations.

Superfamily Troguloidea: The superfamily consists of four families, that is, Nipponopsalididae, Nemastomatidae, Dicranolasmatidae and Trogulidae. Nipponopsalididae includes three described species within the genus *Nipponopsalis* Martens & Suzuki 1966 that occur in Japan and Korea. Nemastomatidae is a morphologically diverse family of about 50 species with a primarily Holarctic distribution (Shear & Gruber 1983; but see Schwendinger & Gruber 1992). The dicranolasmatids include several species within the genus *Dicranolasma* Sörensen 1873 which occurs in southern Europe, southwestern Asia and northern Africa. The trogulids include several genera distributed in Europe, the Caucases, the Middle East and North Africa (Roewer 1923; Shear 1982). Dicranolasmatids and troguloids are similar in having heavily sclerotized bodies, an optic tubercle bearing two anteriorly projecting processes and, in most, in gluing soil particles to the exoskeleton.

Following Martens et al. (1981), the superfamily is represented here by three genera, namely *Paranemastoma* (Nemastomatidae), *Dicranolasma* (Dicranolasmatidae) and *Trogulus* (Latreille 1892) (Trogulidae). Martens et al. examined the ovipositor in four troguloid species, *Paranemastoma quadripunctatum* (Perty 1833), *Dicranolasma scabrum* (Herbst 1799), *Trogulus nepaeformis* (Scopoli 1763) and *T. coriciformis* C.L. Koch 1839. Martens (1986) did not list the species used in his characterization of the troguloid penis and treated this character in general terms at the super-

familial level. Somatic characters for the present analysis were determined for *Paranemastoma sillii* (Herman 1871), *Dicranolasma scabrum* and *Trogulus nepaeformis* from the literature and original observations.

Character analysis.—*Character 1:* Soil crypsis by glandular adhesion of particles: 0, absent; 1, present. Several litter- or soil-dwelling opilions have evolved chemical and/or mechanical specializations for covering their bodies with soil or detritus. *Dicranolasma* and *Trogulus* are unique among the terminal taxa examined here in using a gland-produced adhesive for coating their bodies with soil particles (Shear & Gruber 1983).

Character 2: Medial eye tubercle with anteriorly projecting bilobed hood equipped with marginal fringe of cuticular projections: 0, absent; 1, present. Hoodlike structures projecting anteriorly from the carapace and covering the feeding apparatus have evolved independently in several opilion lineages, e.g., ortholasmatine nemastomatids (Shear & Gruber 1983) and *Ceratolasma* (Gruber 1978). The hood in *Dicranolasma* and *Trogulus* is formed by bilobed processes projecting anteriorly from the eye tubercle and are fringed with leathery cuticular projections (Roewer 1923: figs. 800–806; pers. obs.) Some authors have suggested that the structures are not homologous in the two families, as the eyes are located basally on the hood in *Trogulus* and more distally in *Dicranolasma* (Shear & Gruber 1983). However, presence of basally located eyes in immature *Dicranolasma* (Roewer 1923: fig. 2; Gruber 1996: figs. 16–20) suggests that either the adult condition in *Dicranolasma* is an autapomorphic modification of a more general trogulid condition or that the trogulid state is a paedomorphic expression of the condition in *Dicranolasma*.

Character 3: Metapeltidial cones: 0, absent; 1, present. Metapeltidial cones are small projections that occur on the dorsal surface of the metapeltidium. A pair of metapeltidial cones is present in *Sabacon* (Roewer 1923: fig. 869; Martens 1988: figs. 16–18; pers. obs.) and in *Caddo agilis* and *C. pepperella* (pers. obs.). Metapeltidial cones in *Caddo* appear to have gone unrecognized by previous workers. The cones are readily seen in *C. agilis*, where they are small dark projections located at the lateral margins of the white band on the medial metapeltidial surface. The cones are easily over-

looked in *C. pepperella,* where they are small tubelike processes that are concolorous with the metapeltidium. *Ischyropsalis* species have a variable number of metapeltidial cones (Roewer 1923: figs. 849, 859, 860, 865; Shear 1986; pers. obs.). Shear (1986) described a pair of metapeltidial depressions in *Hesperonemastoma modestum* and hypothesized that these represent vestigial cones. The existence of these depressions could not be corroborated (pers. obs.) and, in any event, the attempt to homologize invaginated depressions with evaginated cones seems questionable.

Character 4: Prosomal intercoxal sternal region: 0, no apparent prosomal intercoxal region; 1, prosomal sternal region flexibly attached to pedal coxae; 2, prosomal sternal region sclerotized with firm attachment to pedal coxae. The ventral surface of the prosoma in Opiliones can be divided into three basic regions, namely, the labium, intercoxal sternal region, and *arculi genitales.* The labium is an apparent sternite associated with the coxae of the first leg pair (Winkler 1957), and the *arculi genitales* forms the dorsoanterior margin of the pre-genital chamber and probably corresponds to the sternite of the first opisthosomal somite (Hansen & Sörensen 1904). The intercoxal sternal region does not appear to be a distinct sclerite, or sternite, but is a region with different degrees of development and sclerotization in different lineages (Pocock 1902; Hansen & Sörensen 1904). The intercoxal sternal region is well developed in *Limulus* (Xiphosura) and is flexibly attached to the pedal coxae by soft cuticle (pers. obs.). The "labium" may correspond to a small sclerite associated with the coxae of leg I in scorpions (Shultz 1990). The "sternum" of scorpions may represent the first opisthosomal sternite (van der Hammen 1986) and, if so, would correspond to the *arculi genitales.* The coxae of legs I and II in scorpions meet along the midline obliterating the prosomal intercoxal sternal region (Shultz 1990).

The sternal region is connected to pedal coxae 2 and 3 by flexible cuticle in *Phalangium* (Hansen & Sörensen 1904: fig. B; pers. obs.), *Caddo* (pers. obs.), *Sabacon* (Hansen & Sörensen 1904; pers. obs.) and *Ischyropsalis* (Pocock 1902: fig. 1B; Roewer 1923: fig. 39; pers. obs.). The sternal region is sclerotized and fused to pedal coxae 2 and 3 in *Peltonychia* (pers. obs.)*, Holoscotolemon* (Roewer

1923; Briggs 1969), *Scotolemon* (van der Hammen 1985: figs. 2, 11), *Vonones* (pers. obs.), *Gonyleptes* (Roewer 1923), *Hesperonemastoma* (pers. obs.), *Paranemastoma* (pers. obs.), *Dicranolasma* (Pocock 1902: fig. 3A; pers. obs.) and *Trogulus* (Pocock 1902: fig. 3B; pers. obs.).

Character 5: Diaphanous cheliceral teeth: 0, absent; 1, present. The opposing margins of the cheliceral fingers are emarginate and lined with diaphanous to subdiaphanous teeth in *Sabacon* (Roewer 1923: fig. 867; Suzuki 1965: fig. 4; pers. obs.), *Ischyropsalis* (Roewer 1923: fig. 849b; Eisenbeis & Wichard 1987: plate 22; pers. obs.), *Hesperonemastoma* (pers. obs.), *Paranemastoma* (Eisenbeis & Wichard 1987: plate 18; pers. obs.), *Dicranolasma* (pers. obs.) and *Trogulus* (Eisenbeis & Wichard 1987: plates 20, 21; pers. obs.).

Character 6: Male cheliceral glands: 0, absent; 1, present. Glands open on the basal cheliceral article in males of *Sabacon* (Martens & Schawaller 1977: fig. 9), *Ischyropsalis* (Martens & Schawaller 1977: figs. 7, 8), *Paranemastoma* (Martens & Schawaller 1977: fig. 6), and most *Dicranolasma* species (Martens & Schawaller 1977: fig. 1).

Character 7: Glandular pedipalpal setae: 0, absent or simple; 1, plumose; 2, clavate. Plumose pedipalpal setae are present in *Phalangium* (pers. obs.), *Caddo* (Gruber 1974: fig. 20a), *Hesperonemastoma* (Shear 1986: fig. 8) and *Sabacon* (Shear 1986: figs. 7, 9). Clavate glandular setae are expressed at some time during postembryonic development in nemastomatids and *Dicranolasma* (Gruber 1978).

Character 8: Pedipalpal apotelic claw: 0, present, readily observed; 1, extremely small or apparently absent. The opilion pedipalp is primitively equipped with a terminal apotelic claw, a condition retained in *Phalangium* (Edgar 1990: figs. 57, 105; pers. obs.), *Caddo* (pers. obs.), *Peltonychia* (pers. obs.), *Holoscotolemon* (Briggs 1969: fig. 7) , *Scotolemon* (van der Hammen 1985: fig. 23), *Vonones* (pers. obs.), *Gonyleptes* (Roewer 1923) and *Oncopus* (Bristowe 1976: plate 1). The claw is greatly reduced or absent in *Siro* (Eisenbeis & Wichard 1987: plate 27; van der Hammen 1985: fig. 23; pers. obs.), *Sabacon* (Martens 1989: figs. 5, 6, 11; pers. obs.), *Ischyropsalis* (pers. obs.), *Hesperonemastoma* (pers. obs.), *Paranemastoma* (pers. obs.), *Dicranolasma* (pers. obs.) and *Trogulus* (pers. obs.).

Character 9: Leg II: 0, not longer than adjacent legs; 1, longer than adjacent legs. Leg II is typically longer than adjacent legs in nonsironoid opilions, including *Peltonychia* (pers. obs.), *Holoscotolemon* (Roewer 1923: p. 102), *Scotolemon* (Roewer 1923: p. 97; Berland 1949: fig. 589), *Vonones* (Shear 1982: plate 102: pers. obs.), *Gonyleptes* (Roewer 1923), *Oncopus* (Bristowe 1976: plate 1), *Phalangium* (Berland 1949: fig. 597: pers. obs.), *Caddo* (pers. obs.), *Ischyropsalis* (Berland 1949: fig. 596; pers. obs.), *Sabacon* (pers. obs.), *Hesperonemastoma* (pers. obs.), *Paranemastoma* (Berland 1949: fig. 595; pers. obs.), *Dicranolasma* (Gruber 1993: figs. 9, 12; pers. obs.) and *Trogulus* (Berland 1949: fig. 594; pers. obs.). Leg II is shorter or not notably longer than adjacent legs in *Siro* and other sironoids (Hansen & Sörensen 1904; pers. obs.).

Character 10: Coxapophysis, leg II: 0, absent; 1, present, not conelike; 2, present, conelike; ?, Xiphosura. Coxapophyses are projections occurring on the medial surface of the pedipalpal and certain pedal coxae (especially legs I and II) in scorpions and many opilions, where they assist in forming a preoral chamber, the stomotheca (Hansen & Sörensen 1904). These structures are typically termed "endites" in the literature, which implies homology with the endites of xiphosurans and eurypterids. However, recent comparative skeletomuscular studies (unpubl. data) indicate that the coxapophyses are more similar to immovable coxal processes of *Limulus* (Xiphosura) than to the endites. Given the uncertainties in homology, van der Hammen suggested that the more neutral term coxapophysis be used in describing these structures, and this usage is adopted here.

The coxapophyses are frequently reduced or lost on the posterior legs in Opiliones, but variation in their expression on leg II may have significance for resolving higher-level relationships. Coxapophyses are present on leg II in *Siro* (Shear 1980: figs. 12,14,21; pers. obs.), *Phalangium* (pers. obs.), *Caddo* (Roewer 1923: fig. 847; pers. obs.), *Ischyropsalis* (Pocock 1902: fig. 1B; Martens & Suzuki 1966: fig. 1; pers. obs.) and *Hesperonemastoma* (pers. obs.). Coxapophyses are also present but variously developed in *Peltonychia* (pers. obs.), *Holoscotolemon* (Roewer 1923: fig. 37), *Scotolemon* (van der Hammen 1985:

figs. 2, 11), *Vonones* (pers. obs.), *Gonyleptes* (Roewer 1923) and *Oncopus* (Roewer 1923: figs. 60–62, 64). Coxapophyses are absent on leg II in *Paranemastoma* (Roewer 1923: fig. 40; pers. obs.), *Dicranolasma* (Pocock 1902: fig. 3A; pers. obs.), *Trogulus* (Pocock 1902: fig. 3B; Roewer 1923: fig. 41; pers. obs.) and most *Sabacon* species (Hansen & Sörensen 1904; pers. obs.). However, Hansen & Sörensen (1904: p. 32) describe *Sabacon* (*Tomicomerus*) *bryanti* (Banks 1898) as having coxapophyses ("low rounded tubercles or thick cones") on leg II. *Sabacon* is coded here as being polymorphic for this character, a decision that assumes Shear (1986) was justified in synonymizing *Tomicomerus* with *Sabacon*. Conelike coxapophyses are also present in *Ischyropsalis* (Pocock 1902: fig. 1B; Martens 1969: fig. 27; pers. obs.) and *Hesperonemastoma* (pers. obs.).

Character 11: Pedal telotarsi: 0, without tarsomeres; 1, with tarsomeres. The telotarsi are undivided in most chelicerates, but they are typically subdivided into numerous tarsomeres in opilions. However, among the terminal taxa examined here, *Siro* (Hansen & Sörensen 1904; pers. obs.) and *Oncopus* (Roewer 1923: fig. 60; Bristowe 1976: plates I, II) have undivided pedal telotarsi. *Trogulus* is polymorphic for the character (Hansen & Sörensen 1904; Roewer 1923: figs.794–799).

Character 12: Pairs of midgut diverticula: 0, no comparable structures; 1, three; 2, four. Midgut diverticula are found in many arachnids, although those of Opiliones appear to have a unique arrangement or are not readily homologized with those of the outgroups. Dumitrescu (1975) has conducted a comparative survey of these structures in Opiliones, and most of the information presented here is derived from that work. Four pairs of midgut diverticula are present in *Siro, Caddo, Ischyropsalis, Sabacon, Hesperonemastoma, Paranemastoma, Dicranolasma, Trogulus* (Dumitrescu 1975) and *Phalangium* (Loman 1903: fig. 20; Berland 1949: fig. 571). All laniatorean opilions examined by Dumitrescu had three pairs of midgut diverticula. However, except for *Peltonychia,* his generic taxon sample did not overlap the one used here. However, as Dumitrescu found three pairs of midgut diverticula in all laniatorean opilions (including a cladonychiid, phalangodid, cosmetid and gonyleptid), the genera *Holoscoto-*

lemon, Scotolemon, Vonones and *Gonyleptes* were coded as having this state, as well. Similarly, Dumitrescu did not include an oncopodoid in his analysis, but *Oncopus* was coded here as having three pairs of midgut caeca, as observed in the oncopodoid *Gnomulus* Thorell 1890 (Loman 1903: fig. 19).

Character 13: Sternite of opisthosomal somite 9: 0, present, well developed; 1, very small or apparently absent. Opisthosomal sternite 9 is present and readily observed in *Siro* (Roewer 1923: fig. 22; pers. obs.), *Peltonychia* (pers. obs.), *Holoscotolemon* (Briggs 1969: fig. 7), *Scotolemon* (van der Hammen 1985: fig. 2), *Vonones* (pers. obs.), *Gonyleptes* (Roewer 1923) and *Oncopus* (Roewer 1923: fig. 60a), although it is generally fused with sternite 8. It is greatly reduced or absent in *Phalangium* (pers. obs.), *Caddo* (pers. obs.), *Sabacon* (pers. obs.), *Ischyropsalis* (pers. obs.), *Hesperonemastoma* (pers. obs.), *Paranemastoma* (Hansen & Sörensen 1904: fig. H; pers. obs.), *Dicranolasma* (pers. obs.) and *Trogulus* (pers. obs.).

Character 14: Opisthosomal tergite 9 divided dorsally: 0, absent; 1, present. Following the interpretation of Hansen & Sörensen (1904), the dorsal surface of the opilion opisthosoma is generally regarded has having nine tergites and an anal operculum. Tergite 9 is variously modified in Opiliones in association with specializations of the anal complex. It is undivided in *Siro* and other sironids, whether distinct or consolidated in various ways with adjacent tergites and sternites (Hansen & Sörensen 1904; Roewer 1923: fig. 22; Shear 1980; pers. obs.). It is also undivided in *Peltonychia* (pers. obs.), *Holoscotolemon* (Briggs 1969: fig. 7), *Scotolemon* (van der Hammen 1985: fig. 2, but numbering is not precise), *Vonones* (pers. obs.) and *Gonyleptes* (Roewer 1923), but, again, is generally fused to tergite 8. In contrast, tergite 9 in most other opilions is divided dorsally with the two parts widely separated by the anal operculum and, in some cases, by tergite 8. This condition is present *Phalangium* (pers. obs.), *Caddo* (pers. obs.), *Sabacon* (pers. obs.), *Ischyropsalis* (pers. obs.), *Hesperonemastoma* (pers. obs.), *Paranemastoma* (Eisenbeis & Wichard 1987: plate 19; pers. obs.), *Dicranolasma* (pers. obs.) and *Trogulus* (pers. obs.).

Character 15: Genital operculum: 0, no comparable structure; 1, small, not forming

complete floor to pre-genital chamber; 2, well developed, forming complete floor to pre-genital chamber. The structure of the genital operculum in Opiliones is apparently unique and cannot be readily homologized with genital features in other arachnids. The genital operculum in most opilions is an oblong plate or dorsoventrally flattened process that projects anteriorly from the sternite of postoral somite IX and forms the floor to the genital opening or, more precisely, the opening to the pre-genital chamber. A similar situation is present in *Siro* and other sironoids, but the operculum itself is much shorter and only covers the extreme posterior part of the pre-genital opening (Hansen & Sörensen 1904; Eisenbeis & Wichard 1987: plate 27; pers. obs.). Some workers do not regard *Siro* as having a genital operculum (e.g., Shear 1982; Hennig 1986).

Character 16: Differentiation of shaft and glans within spermatopositor/penis: 0, no spermatopositor/penis; 1, shaft and glans absent; 2, shaft and muscle-operated glans; 3, shaft and hydraulically operated glans (Martens 1986). The term "spermatopositor" follows van der Hammen (1985) and refers to the homolog of the penis in sironoids. There is no evidence that the structure in sironoids serves as an intromittent organ.

Character 17: Intrinsic spermatopositor/penis muscles: 0, no spermatopositor/penis; 1, spermatopositor/penis without muscles; 2, spermatopositor/penis with one muscle; 3, spermatopositor/penis with two muscles; 4, spermatopositor/penis with at least three muscles. (Martens 1986).

Character 18: External morphology of ovipositor: 0, no ovipositor; 1, cuticular annuli, setae along shaft, terminal sensory organs; 2, without cuticular annuli, setae along shaft, no terminal sensory organs; 3, without cuticular annuli, few or no setae along shaft, no terminal sensory organs (Martens et al. 1981).

Character 19: Number of distal lobes on ovipositor: 0, no ovipositor; 1, two; 2, four (Martens et al. 1981).

Character 20: Inner sheath of ovipositor lined with cuticular hooks: 0, no ovipositor; 1, absent; 2, present (Martens et al. 1981).

Character 21: Vaginal glands in ovipositor; 0, no ovipositor; 1, aciniform glands; 2, aggregate glands; 3, glands opening without ducts via vaginal pore fields. Martens et al. (1981) noted small glands draining into the

vaginal lumen via small ducts (aciniform glands) in *Paranemastoma, Dicranolasma* and *Trogulus.* Similar glands were drained collectively by larger ducts (aggregate glands) in *Siro, Phalangium, Caddo, Ischyropsalis, Hesperonemastoma* and *Sabacon.* The glands were found to empty directly into the vaginal lumen via pore fields in the vaginal wall in *Peltonychia, Holoscotolemon, Scotolemon, Vonones* and the gonyleptid. The condition in *Oncopus* appears to be intermediate between the aciniform and pore field conditions and is coded here as polymorphic.

Character 22: Seminal receptacles in vaginal lumen of ovipositor: 0, no ovipositor; 1, simple blind sacs or diverticula; 2, encased within structure protruding into vaginal lumen (Martens et al. 1981).

Character 23: Outer longitudinal muscles of ovipositor: 0, no ovipositor; 1, with segmental pattern of insertion; 2, without segmental pattern of insertion (Martens et al. 1981).

Character 24: Outer circular muscles: 0, no ovipositor; 1, absent; 2, present (Martens et al. 1981).

Character 25: Inner longitudinal muscles of ovipositor: 0, no ovipositor; 1, absent; 2, present. Martens et al. (1981) found longitudinal muscles immediately external to the vagina and internal to the circumvaginal muscles in *Scotolemon, Vonones, Oncopus* and a gonyleptid. They noted that the muscles were absent in *Peltonychia* and *Holoscotolemon,* and their figures indicated that inner longitudinal muscles were absent in *Phalangium, Caddo, Ischyropsalis, Hesperonemastoma, Sabacon, Paranemastoma, Dicranolasma* and *Trogulus.* Martens et al. did not report or illustrate the condition in *Siro,* but original examinations of the ovipositor in *Siro acaroides* indicated that inner longitudinal muscles are absent.

Character 26: Ovipositor with X-shaped vaginal lumen and circumferential fold: 0, no ovipositor; 1, absent; 2, present (Martens et al. 1981).

Tree construction.—The phylogenetic program PAUP, v. 3.1.1 (Swofford 1993) was used for all phylogenetic analyses. The data matrix shown in Table 1 was analyzed using the branch-and-bound algorithm, which ensures recovery of all minimal-length trees. All characters were unordered and weighted equally. Entries for multistate taxa were treat-

ed as polymorphisms. Phylogenetic analysis of unweighted data was followed by successive weighting in which each character was initially weighted with the consistency index assigned in the unweighted analysis. Successive weighting was repeated using the retention index.

Evidential support for internal relationships within minimal-length trees was assessed with the decay index (Bremer 1988) and bootstrap analysis (Felsenstein 1985; Hillis & Bull 1993). The decay index was determined for each phylogenetic relationship within a most-parsimonious tree by finding that minimal-length tree that does not contain the relationship. This was accomplished by importing a constraint tree that defined only the proposed relationship and then conducting a branch-and-bound search to discover the shortest tree that does not have the specified relationship. The decay index was calculated by subtracting the length of the most-parsimonious tree from that of the minimal-length constraint-enforced tree. The bootstrap is a nonparametric statistical procedure in which multiple character matrices are assembled by sampling characters from the original with replacement. The new matrices are treated as "independent" samples of the "population" of characters from which the original data were drawn. Bootstrap values were obtained from PAUP and were based on 1000 replicates using simple heuristic searches.

The effect of character class on phylogenetic reconstruction was examined by separate analysis of somatic characters (Table 1: characters 1–15) and genitalic characters (Table 1: characters 16–26). Again, these analyses were conducted using the branch-and-bound algorithm, but decay indices and bootstrap values were not determined. Rather, relationships were depicted as 50% majority-rule consensus trees, which show the relationships recovered in 50% or more of the minimal-length trees recovered.

RESULTS

Parsimony analysis of the data matrix in Table 1 yielded two minimal-length trees (tree length = 61; consistency index = 0.82, retention index = 0.90) which differed only with respect to their placement of *Hesperonemastoma*, which was either 1) the sister group to *Ischyropsalis* and *Sabacon* or 2) the sister

group to ((*Ischyropsalis, Sabacon*), (*Paranemastoma*, (*Dicranolasma, Trogulus*))). Only the former alternative is illustrated in Fig. 1 because it is the single most parsimonious topology resulting from successive weighting using consistency index (tree length = 50502, consistency index = 0.88, retention index = 0.94) and retention index (tree length = 51765, consistency index = 0.86, retention index = 0.93).

Analysis of somatic (non-genitalic) characters (Table 1: characters 1–15) produced six minimal length trees (tree length = 30, consistency index = 0.73, retention index = 0.86) and the 50% majority-rule consensus tree is illustrated in Fig. 3. Relationships among terminal taxa within Laniatores (*Peltonychia, Holoscotolemon, Scotolemon, Vonones, Gonyleptes, Oncopus*) were unresolved. The remaining relationships were consistent with those recovered by the full data set, except that *Hesperonemastoma* was consistently reconstructed as the sister to ((*Ischyropsalis, Sabacon*), (*Paranemastoma*, (*Dicranolasma, Trogulus*))). Successive-weighting analysis produced the same six minimal-length trees as the unweighted data using both consistency and retention indices.

Analysis of genitalic characters (Table 1: characters 16–26) produced 82 minimal-length trees (tree length = 29, consistency index = 0.97, retention index = 0.98). The 50% majority-rule consensus tree (Fig. 3) showed that genitalic characters recovered superfamilies in over 50% of the minimal-length trees and reconstructed *Siro* as sister to a clade containing *Phalangium* and *Caddo*. The strict consensus tree can be visualized by collapsing those relationships not observed in 100% of the minimal-length trees. Consequently, a strict consensus of the 82 trees would show no phylogenetic resolution within Opiliones. Successive weighting using consistency and retention indices produced trees identical to those recovered by the unweighted data.

DISCUSSION

Opilion phylogeny.—Results from this analysis are inconsistent with the Cyphopalpatores concept, which regards Cyphophthalmi as the sister group to a subset of palpatorean opilions and considers Palpatores to be a paraphyletic assemblage. Specifically, parsimony reconstructed the cyphophthalmid *Siro*

Table 1.—Character matrix used in the present analysis. Polymorphisms (e.g., "1/2") were assigned to genera that express two relevant states in different species. The uncertainty ("?") assigned to *Limulus* is explained in the text.

Taxa / Characters	Xipho-sura	Scorpi-ones	Siro	Pelto-nychia	Holosco-tolemon	Scoto-lemon	Vonones	Gony-leptes	Oncopus	Phalan-gium	Caddo	Is-chyrop-salis	Sabacon	Hes-pero-nemas-toma	Para-nema-stoma	Dicra-nolas-ma	Trog-ulus
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
3	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0
4	1	0	0	2	2	2	2	2	2	1	1	1	1	2	2	2	2
5	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	1
6	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	2	0
7	0	0	0	0	0	0	0	0	0	1	1	1	1	1	2	1	0
8	0	0	1	0	1	0	0	0	0	0	0	1	1	1	1	1	1
9	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1
10	?	0	1	1	1	1	1	1	1	1	1	2	0/2	2	0	1	0
11	0	0	0	1	1	1	1	1	0	1	1	1	1	1	1	2	0/1
12	0	0	2	0	0	0	0	0	1	2	2	2	2	2	2	1	2
13	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1
14	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1
15	0	0	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2
16	0	0	1	2	2	3	3	3	3	2	2	2	2	2	2	2	2
17	0	0	4	2	2	3	1	1	1	2	2	2	2	2	3	3	3
18	0	0	1	3	3	3	3	3	3	1	2	3	3	3	2	2	2
19	0	0	1	2	2	1	1	1	1	1	1	1	1	1	1	1	1
20	0	0	2	1	1	3	1	1	1	2	2	1	1	1	1	1	1
21	0	0	1	3	3	3	3	3	1/3	2	1	2	2	2	2	2	2
22	0	0	1	1	1	1	1	1	1	1	1	2	2	2	1	1	1
23	0	0	1	2	2	2	2	2	2	1	1	2	2	2	2	2	2
24	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
25	0	0	1	1	1	2	2	2	2	1	1	1	1	1	1	1	1
26	0	0	1	2	2	2	2	2	2	1	1	1	1	1	1	1	1

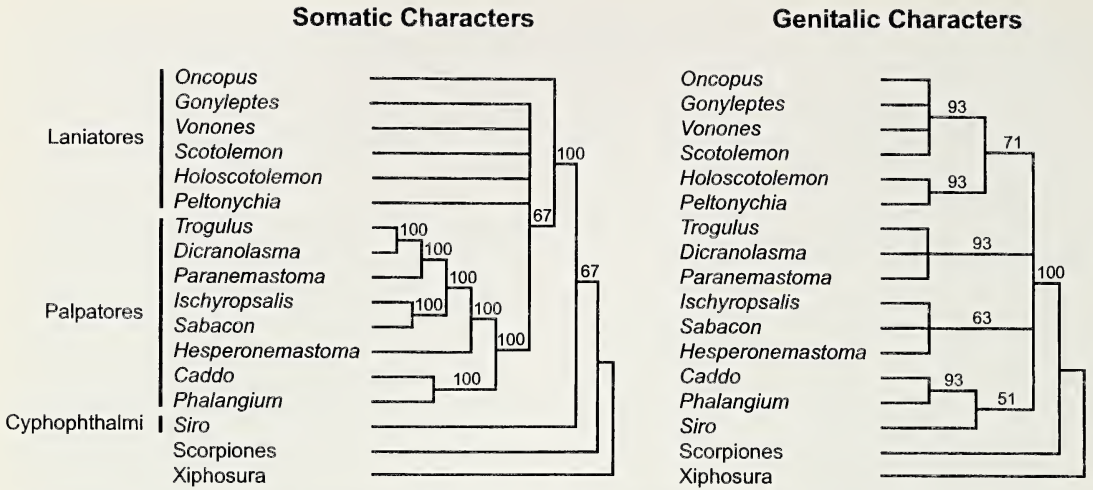**Somatic Characters**   **Genitalic Characters**

Figure 3.—Comparison of 50% majority-rule consensus trees based on 26 characters (Table 1), including 15 somatic characters (Table 1: characters 1–15) and 11 genitalic characters (Table 1: characters 16–26). Somatic characters resolved non-sironoid opilions and Palpatores in 100% of the eight minimal-length topologies but did not resolve Laniatores or relationships among laniatoreans. Genitalic characters recovered Opiliones in 100% of 82 minimal-length trees, and most superfamilies were resolved in over 50% of equally parsimonious trees. Strict consensus trees can be visualized by collapsing those internodes not found in 100% of minimal length trees.

as the sister group to the other opilions and Palpatores as the monophyletic sister group to Laniatores. A further implication of the Cyphopalpatores concept is that Ischyropsalidoidea and Troguloidea do not form a monophyletic group (Dyspnoi) that other opilion systematists have recognized (e.g., Juberthie & Manier 1978). However, results from the present analysis are concordant with the Dyspnoi hypothesis. The degree to which the Cyphopalpatores concept differs from the topology generated here can be illustrated by finding the minimal-length tree that contains all superfamily relationships proposed by Martens et al. This was accomplished by enforcing a "Cyphopalpatores" constraint tree during branch-and-bound analysis of the full data matrix (Table 1). The analysis produced two minimal-length topologies that differed only with respect to generic relationships within Troguloidea (Length = 68, consistency index = 0.73, retention index = 0.84). The minimal-length Cyphopalpatores tree was seven steps longer than the most-parsimonious solution and represents only two of the over 4000 possible solutions of the same length.

While the minimal-length tree favored here is clearly in conflict with the Cyphopalpatores concept, it does not represent a com-

pelling solution to higher-level relationships within Opiliones. A much larger sampling of taxa and characters is needed. Still, these results are congruent with those from other studies. For example, ultrastructural analyses have shown that spermatozoa of the cyphophthalmid *Siro rubens* retain non-motile axonemes but that virtually all flagellar elements are absent in the palpatorean and laniatorean opilions that have been examined (Juberthie & Manier 1978). Because presence of a flagellum is undoubtedly primitive in Chelicerata (Shultz 1990), absence of this structure may be a synapomorphic feature of Palpatores and Laniatores. Further, the epistome-pharynx apparatus has been examined in representatives of the three opilion suborders and results are concordant with that derived from sperm ultrastructure (unpubl. data). Specifically, the epistomes in scorpions and *Siro* (Cyphophthalmi) have one dorsal and two lateral arms that serve as attachments for pharyngeal dilator muscles. However, the epistome essentially surrounds the pharynx in *Leiobunum aldrichi* (Weed 1893) (Palpatores: Phalangioidea) and *Acromares banks* Goodnight & Goodnight 1942 (Laniatores: Gonyleptoidea) such that fibers of the pharyngeal
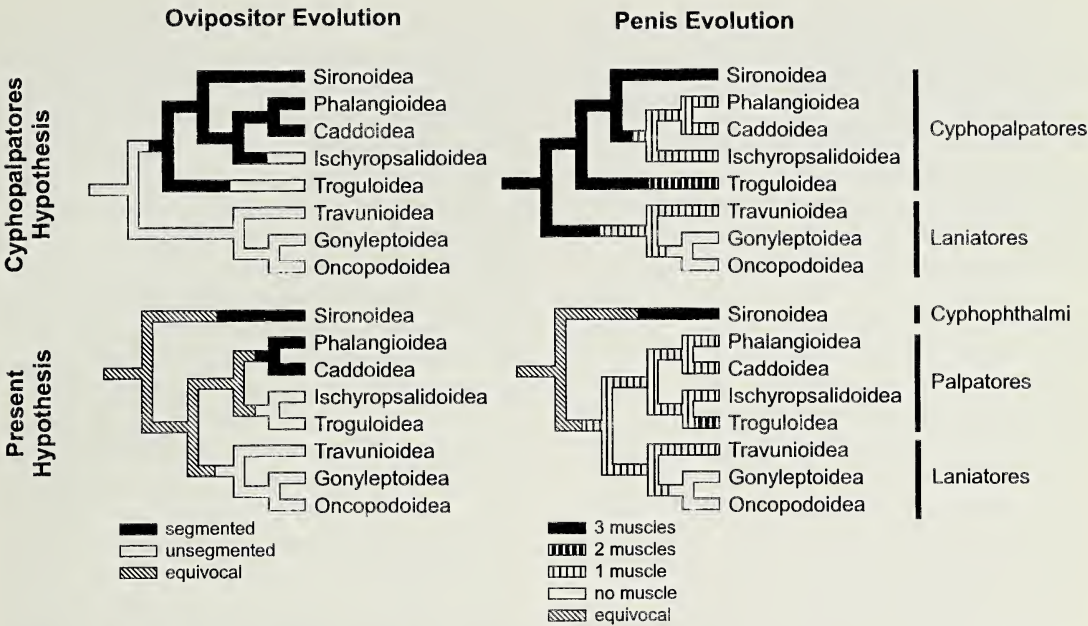
Figure 4.—Evolution of ovipositor segmentation and intrinsic spermatophore/penis muscles according to two scenarios.

dilators radiate from the full circumference of the pharynx.

Genitalic evolution.—The analysis of opilion phylogeny offered by Martens et al. was based almost exclusively on speculative transformation series of genitalic characters. The first cladogenetic event in the Cyphopalpatores hypothesis (Figs. 1, 4) resulted in the separation of Laniatores and Cyphopalpatores, with Laniatores retaining a "primitively unsegmented" ovipositor and Cyphopalpatores developing an ovipositor with cuticular annuli (Fig. 4). Martens et al. suggested that Troguloidea was the first clade to diverge within Cyphopalpatores, even though Troguloidea is characterized by ovipositors that *lack* cuticular segmentation. Martens et al. cited presence of a segmental pattern of muscle insertions in troguloids as evidence for primitive cuticular segmentation in the troguloid ancestor and thereby attempted to justify the use of the segmented ovipositor as a synapomorphy of Cyphopalpatores. Martens et al. argued further that the segmented ovipositor was also lost secondarily in the Ischyropsalidoidea but this time along with all internal evidence of segmentation, as well. This evolutionary scenario begs two questions. First, how did Martens et al. discriminate *a priori* between an ovipositor

that lacks all evidence of segmentation due to primitive absence (Laniatores) from one that lacks all evidence of segmentation due to secondary loss (Ischyropsalidoidea)? Second, how can one know that segmentally arranged muscle attachment must accompany or follow cuticular segmentation rather than precede this condition? Convincing answers to both questions were necessary in formulating their transformation series and their phylogenetic conclusion, but Martens et al. did not offer them.

In reconstructing the evolution of the spermatopositor/penis, Martens et al. reasoned that the short, three-muscle condition in sironoids was primitive for Opiliones, apparently because it alone had the potential to generate other conditions by the loss of muscles. Specifically, the one-muscle penis could have evolved through loss of the two lateral muscles of sironoids, and the two-muscle penis could have arisen through loss of the median muscle (Fig. 4). Because Martens et al. regarded sironoids as a late-divergent group, the one-muscle condition must have arisen from the three-muscle condition at least twice; once in basal laniatoreans and once in the common ancestors of phalangioids, caddoids and ischyropsalidoids.

An alternative and more objective strategy for understanding genitalic evolution is to reconstruct phylogeny using as many characters as possible, except the character of interest, and then to superimpose the character on the resulting topology to determine its course of evolution. This analysis was undertaken here for the characters of ovipositor segmentation and numbers of intrinsic penial muscles.

To reconstruct evolution of the ovipositor, character 18 was excluded from the matrix in Table 1 and analyzed in PAUP using the branch-and-bound algorithm. The resulting trees were identical to those achieved using the full matrix (tree length = 57, consistency index = 0.82, retention index = 0.91). The program MacClade, 3.1 (Maddison & Maddison 1992) was used to determine the most-parsimonious distribution of the binary character "ovipositor segmentation." The results indicate that the primitive state of the opilion ovipositor is unclear given current information. It is equally parsimonious to conclude that, 1) the opilion ovipositor was originally segmented and that segmentation was lost twice or, 2) that the ovipositor was originally unsegmented and evolved segmentation twice. Current evidence would tend to favor the former, given the other complex similarities between the ovipositors of sironoids, phalangioids and caddoids (e.g., terminal lobes and sensory organs, colleterial glands) and the segmental patterns of muscle insertions in troguloids.

The evolution of intrinsic penial muscles was examined in a similar way, but, in this case, character 17 was omitted from the analysis. As in the analysis of ovipositor segmentation, the analysis produced two minimal-length trees identical to those recovered from analysis of the full data set (tree length = 57, consistency index = 0.81, retention index = 0.90). Character 17 was then superimposed on the topology in Fig. 2 using MacClade. The primitive state of the intrinsic penial muscles is unclear from this analysis; it may have been a three-muscle or one-muscle penis. In either case, one need only invoke a single origin for the one-muscle penis, with the two-muscle penis of troguloids and the non-muscular penis of laniatoreans having evolved from the one-muscle condition.

It is interesting to note that the transformation series in ovipositor and spermatopos-

itor/penis evolution favored by Martens et al. are largely compatible with those found by parsimony analysis. The hypothesis that the unsegmented ovipositors of ischyropsalidoids and troguloids evolved from a segmented ovipositor is one of the two equally parsimonious transformation series suggested by the present analysis. However, while Martens et al. regarded the unsegmented condition in Laniatores as primitive, the present analysis would suggest that it represents a secondary loss of segmentation. One could also argue that Laniatores has a primitively unsegmented ovipositor, but this position would require independent origin of segmentation in Sironoidea and the ancestors of the Phalangioidea-Caddoidea clade. The transformation series that Martens et al. proposed for the evolution of intrinsic penial muscles is also largely congruent with results derived from parsimony. The hypotheses that the one-muscle penis evolved from a three-muscle penis and that the nonmuscular penis evolved from a one-muscle penis are consistent with results of the present analysis, the principal difference being the frequency of the three-muscle to one-muscle transformations. In contrast, the two scenarios differ in explaining the origin of the two-muscle penis of troguloids. Martens et al. propose that it evolved from reduction in the three-muscle penis, and parsimony suggests that it originated from the one-muscle condition.

These results suggest that a given character transformation series can be compatible, or largely compatible, with two or more phylogenetic topologies. In the absence of information from other characters, it would be difficult to recognize or discriminate among these alternative topologies. The principal conclusion of this analysis is that the Cyphopalpatores concept was based on reasonable interpretations of genitalic character evolution but that these interpretations were used to support only one of several possible topologies that were broadly consistent with the proposed transformation series. Parsimony-based analysis of genitalic and non-genitalic characters recovered a topology that was largely concordant with the transformation series upon which the Cyphopalpatores concept was erected but recovered a different phylogenetic topology that was based on a more objective and empirically robust analysis.

LITERATURE CITED

Berland, L. 1949. Ordre des Opilions, Pp. 761–793. *In* Traité de Zoologie, VI. (P.-P. Grassé, ed.). Masson, Paris.

Bremer, K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. Evolution, 42:795–803.

Briggs, T.S. 1969. A new Holarctic family of laniatorid phalangids (Opiliones). Pan-Pacific Entomol., 45:35–50.

Bristowe, W.S. 1976. Rare arachnids from Malaysia and Sumatra. J. Zool., London, 178:7–14.

Cokendolpher, J.C. & E.A. Maury. 1990. *Austropsopilio* harvestmen (Opiliones, Cyphopalpatores, Caddidae) discovered in South America. Bol. Soc. Biol. Concepción, 61:59–62.

Crosby, C.R. 1911. A new species of Phalangida from Missouri. Canadian Entomol., 43:20–22.

Dumitrescu, D. 1975. Contribution à l'étude morphologique de l'appareil digestif (intestin moyen) des Opilions. Proc. 6th Int. Arachnol. Congr., 1974, Amsterdam:150–154.

Edgar, A.L. 1990. Opiliones (Phalangida). Pp. 529–581. *In* Soil Biology Guide, (D.L. Dindal, ed.). John Wiley & Sons, New York.

Eisenbeis, G. & W. Wichard. 1987. Atlas on the Biology of Soil Arthropods. Springer Verlag, Berlin.

Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution, 39:783–791.

Gruber, J. 1970. Die "Nemastoma" Arten Nordamerikas (Ischyropsalididae, Opiliones, Arachnida). Ann. Naturhist. Mus. Wien, 74:129–144.

Gruber, J. 1974. Bemerkungen zur Morphologie und systematischen Stellung von *Caddo, Acropsopilio* und verwandter Formen (Opiliones, Arachnida). Ann. Naturhistor. Mus. Wien, 78: 237–259.

Gruber, J. 1978. Redescription of *Ceratolasma tricantha* Goodnight and Goodnight, with notes on the family Ischyropsalididae (Opiliones, Palpatores). J. Arachnol., 6:105–124.

Gruber, J. 1993. Beobachtungen zur Ökologie und Biologie von *Dicranolasma scabrum* (Herbst, 1799). Teil I. Ann. Naturhist. Mus. Wien, 94/95B:393–426.

Gruber, J. 1996. Beobachtungen zur Ökologie und Biologie von *Dicranolasma scabrum* (Herbst, 1799). Teil II: Fortpflanzung, Entwicklung und Wachstum. Ann. Naturhist. Mus. Wien, 98B:71–110.

Hansen, H.J. & W. Sörensen. 1904. On Two Orders of Arachnida. Cambridge University Press, Cambridge.

Hillis, D.M. & J.J. Bull. 1993. An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. Syst. Biol., 42:182–192.

Hennig, W. 1986. Wirbellose II: Gliedtiere.: Harri Deutsch, Thun and Frankfurt/Main.

Hoheisel, U. 1980. Anatomie und taxonomische Bedeutung der Legeröhre der Opiliones. Verh. 8. Intern. Arachn. Kongr. Wien, pp. 315–318.

Juberthie, C. & J.-F. Manier. 1978. Etude ultrastructural comparée de la spermiogenèse des opilions et son intéræt phylétique. Symp. Zool. Soc. London, No. 42:407–416.

Loman, J.C.C. 1903. Vergleichend anatomische Untersuchungen an chilenischen und andern Opilioniden. Zool. Jb., Suppl., 6:115–199.

Maddison, W.P. & D.R. Maddison. 1992. MacClade: Analysis of Phylogeny and Character Evolution. Version 3.0. Sinauer Associates, Sunderland, Massachusetts.

Martens, J. 1969. Die Abgrenzung von Biospezies auf biologisch-ethologischer Grundlage am Beispiel der Gattung *Ischyropsalis* C.L. Koch 1839 (Opiliones, Ischyropsalididae). Zool. Jb. Syst., 96:133–264.

Martens, J. 1976. Genitalmorphologie, System und Phylogenie der Weberknechte (Arachnida: Opiliones). Entomol. Germanica, 3:51–68.

Martens, J. 1978. Weberknechte, Opiliones. Tierwelt Deutschland, 64:1–464.

Martens, J. 1980. Versuch eines phylogenetischen Systems der Opiliones. Verh. 8. Intern. Arachn. Kongr. Wien, pp. 355–360.

Martens, J. 1986. Die Grossgliederung der Opiliones und die Evolution der Ordnung (Arachnida). Actas X Congr. Int. Arachnol, Jaca/España, I:289–310.

Martens, J. 1988. Fissiphalliidae, a new family of South American laniatorean harvestmen (Arachnida: Opiliones). Z. Zool. Syst. Evol., 26:114–127.

Martens, J. 1989. Sibirische Arten der Gattung *Sabacon* Simon 1879. Senckenbergiana Biol., 69: 369–377.

Martens, J., U. Hoheisel & M. Götze. 1981. Ver-

gleichende Anatomie der Legeröhren der Opiliones als Beitrag zur Phylogenie der Ordnung (Arachnida). Zool. Jb. Anat., 105:13–76.

Martens, J. & W. Schawaller. 1977. Die Cheliceren-Drüsen der Weberknechte nach rasteroptischen und lichtoptischen Befunden (Arachnida: Opiliones). Zoomorphologie, 86:223–250.

Martens, J. & S. Suzuki. 1966. Zur systematischen Stellung ostasiatischer Ischyropsalididen-Arten (Arachnoidea, Opiliones, Ischyropsalididae). Annot. Zool. Japonica, 39:215–221.

Pocock, R.I. 1902. Some points in the morphology and classification of the Opiliones. Ann. Mag. Nat. Hist., Series 7, 10:504–516.

Roewer, C.-F. 1923. Die Weberknechte der Erde. Gustav Fischer, Jena.

Savory, T.H. 1971. Evolution in the Arachnida. Merrow, Bath.

Schwendinger, P.J. & J. Gruber. 1992. A new *Dendrolasma* (Opiliones, Nemastomatidae) from Thailand. Bull. British Arachnol. Soc., 9:57–60.

Selden, P.A. 1990. Fossil history of the arachnids. Newsl. British Arachnol. Soc., No. 58:4–6.

Shear, W.A. 1980. A review of the Cyphophthalmi of the United States and Mexico, with a proposed reclassification of the suborder (Arachnida, Opiliones). American Mus. Nov., No. 2705:1–34.

Shear, W.A. 1982. Opiliones. Pp. 104–110, *In* Synopsis and Classification of Living Organisms, Vol. 2. (S.P. Parker, ed.). McGraw-Hill, New York.

Shear, W.A. 1986. A cladistic analysis of the opilionid superfamily Ischyropsalidoidea, with descriptions of the new family Ceratolasmatidae, the new genus *Acuclavella,* and four new species. American Mus. Nov., No. 2844:1–29.

Shear, W.A. 1996. *Hesperopilio mainae,* a new genus and species of harvestman from Western Australia (Opiliones: Caddidae: Acropsopilioninae). Rec. Western Australia Mus., 17:455–460.

Shear, W.A. & J. Gruber. 1983. The opilionid subfamily Ortholasmatinae (Opiliones, Troguloidea, Nemastomatidae). American Mus. Nov., No. 2757:1–65.

Shultz, J.W. 1990. Evolutionary morphology and phylogeny of Arachnida. Cladistics, 9:1–32.

Šilhavý, V. 1961. Die Grundsátze der modernen Weberknechttaxonomie und Revision des bisherigen Systems der Opilioniden. Verh. 11. Intern. Kongr. Entomol. Wien, 1960, 1:262–267.

Suzuki, S. 1965. Three species of Ischyropsalidae (Phalangida) from Hokkaido. Annot. Zool. Japonica, 38:39–44.

Swofford, D.L. 1993. PAUP: Phylogenetic Analysis Using Parsimony, version 3.1. Smithsonian Institution, Washington, D.C.

van der Hammen, L. 1985. Comparative studies in Chelicerata. III. Opilionida. Zool. Verhand., Leiden, No. 220:1–60.

van der Hammen, L. 1986. Comparative studies in Chelicerata. IV. Apatellata, Arachnida, Scorpionida, Xiphosura. Zool. Verhand., Leiden, No. 226: 1–52.

Weygoldt, P. & H.F. Paulus. 1979. Untersuchungen zur Morphologie, Taxonomie und Phylogenie der Chelicerata. Z. Zool. Syst. Evol., 17:85–116, 177–200.

Winkler, D. 1957. Die Entwicklungen der äusseren Körpergestalt bei den Phalangiidae (Opiliones). Mitt. zool. Mus. Berlin, 33:355–389.

Yoshikura, M. 1975. Comparative embryology and phylogeny of Arachnida. Kumamoto J. Sci. (Biology), 12:71–142.

NEW SPECIES OF *CHARON* (AMBLYPYGI, CHARONTIDAE) FROM NORTHERN AUSTRALIA AND CHRISTMAS ISLAND

Mark S. Harvey[1] and **Paul L.J. West**[2]:   Department of Terrestrial Invertebrates, Western Australian Museum, Francis Street, Perth, Western Australia 6000, Australia

ABSTRACT.   Three new species of the genus *Charon* Karsch 1879 are described: *Charon oenpelli* from humid sandstone caves in the Northern Territory, *Charon trebax* from an epigean locality in north Queensland, and *C. gervaisi* from Christmas Island, an Australian territory situated in the Indian Ocean. The status of species formerly attributed to the genus and currently synonymized with the type species *C. grayi* is discussed.

The amblypygid genus *Charon* was first recognized by Karsch (1879) who included a single species from the Philippines, *Phrynus grayi* Gervais 1842, the holotype of which is lodged in the Museum of Natural History, London (Butler 1873). The meager descriptions presented by Gervais (1842, 1844) have since been supplemented by illustrations of the chelicera (Butler 1873), pedipalps (Kraepelin 1895, 1899; Quintero 1986; Weygoldt 1996) and legs (Kraepelin 1899). Seven further species have been added to the genus, but two of these have been subsequently transferred to other genera: *Charon sarawakensis* Thorell 1888 was included in the newly erected genus *Sarax* by Simon (1892), along with the type species *S. brachydactylus* Simon 1892; and *Charon cavernicola* Thorell 1889, was designated the type species of *Stygophrynus* Kraepelin 1895.

Karsch (1880) interpreted the description of *Phrynus medius* (Herbst 1797) (now *Damon medius*) by Hoeven (1842) as representing a separate species, which he named *Charon hoeveni* Karsch. Hoeven's description is relatively good and appears to represent a valid species of *Charon*. Thorell (1888) added three further species based on material collected from Ambon, Indonesia (*C. beccarii* Thorell 1888 and *C. subterraneus* Thorell 1888) and New Guinea (*C. papuanus* Thorell 1888), which were supplemented by extensive and detailed descriptions. *Charon annulipes* Lau-

terer 1895 was described from Brisbane, Queensland. This species is now considered a *nomen dubium* (Harvey 1985), as the type is presumed lost, the original description is woeful, and no further specimens have been collected in Brisbane or any other portion of southeastern Queensland (Monteith 1965). We feel that its true identity will never be known.

Kraepelin (1895, 1899) subsequently synonymized *Charon hoeveni, C. beccarii, C. subterraneus* and *C. papuanus* under the single name *C. grayi,* and presented an illustrated redescription based upon 51 specimens from 22 different localities ranging from Malaysia to the Solomon Islands, noting significant differences which he ascribed to intraspecific variation. As discussed in detail below, we feel that Kraepelin's decision was flawed and that many of these names will be shown to be valid. Kraepelin's polytypic species concept was applied to other amblypygid genera which subsequent authors have rejected as a gross over-simplification of species-level taxonomy in these groups (Gravely 1915; Mullinex 1975; Quintero 1981).

The recent discovery of specimens of *Charon* from sandstone caves in the Northern Territory (Webber 1992) and from epigean localities in northern Queensland and Christmas Island are the first definitive records of the genus from Australia. These three species are formally described here.

METHODS

The specimens examined during the course of this study are lodged in the following institutions: Natural History Museum, London (BMNH), Museum of Tropical Queensland,

[1]To whom all correspondence should be addressed.
[2]Present address: Halpern Glick & Maunsell Pty Ltd, 629 Newcastle St, Leederville, Werstern Australia 6007, Australia

Townsville (MTQ), Museum and Art Gallery of the Northern Territory, Darwin (NTM), Queensland Museum, Brisbane (QM), Swedish Museum of Natural History, Stockholm (SMNH) and Western Australian Museum, Perth (WAM).

Morphological terminology basically follows Quintero (1981) and Weygoldt (1996), except for the pedipalp segments which follow Snodgrass (1948), Shear et al. (1987), Shultz (1989) and Harvey (1992). The six pedipalpal segments are here named (with Quintero's divergent names in parentheses): coxa, trochanter, femur, patella (tibia), tibia (basitarsus) and tarsus. The tarsus is further divided in some amblypygids. The seven basic leg segments (Shultz 1989; Quintero 1981; Weygoldt 1996) are termed: coxa, trochanter, femur, patella, tibia, metatarsus (basitarsus) and tarsus. The first leg is modified into an antenniform appendage, in which the tibia and tarsus are greatly subdivided. Tibiae II-IV are subdivided into a basitibia and distitibia, of which the former is often further divided. Tarsi II-IV are also subdivided.

The female genitalia were examined after clearing in 50% lactic acid at room temperature before viewing under a compound microscope.

Genus *Charon* Karsch

Charon Karsch 1879: 197; Simon, 1892: 47–48; Kraepelin 1895: 41–42; Kraepelin 1899: 247; Gravely 1915: 446; Mello-Leitão 1931: 52 (type species by original designation *Phrynus grayi* Gervais 1842).

Diagnosis.—The combined presence of pulvillae on tarsi II–IV and an undivided pedipalpal tarsus distinguishes *Charon* from all other amblypygids.

Remarks.—The Charontidae were redefined by Quintero (1986) who included only *Charon* and *Stygophrynus*. The remaining genera formerly placed in the Charontidae (*Catageus* Thorell 1889, *Charinus* Simon 1892, *Paracharon* Hansen 1921, *Phrynichosarax* Gravely 1915, *Sarax* Simon 1892 and *Tricharinus* Quintero 1986) were transferred to the new family Charinidae which was hypothesized to represent the sister-group to the Charontidae. The separation of the two families was supported by Weygoldt (1996) who, as part of a detailed cladistic analysis of the Amblypygi, regarded the Charontidae as the

sister-group to the Phrynoidea (Phrynichidae + Phrynidae). *Paracharon* was placed in its own family, Paracharontidae, as the only member of the suborder Paleoamblypygi. *Charon* is the only amblypygid which possesses both tarsal pulvillae and an undivided pedipalpal tarsus (Quintero 1986; Weygoldt 1996).

As discussed above, all previously described species of *Charon* not transferred to other genera or formally designated as *nomina dubia* were synonymized with *C. grayi* by Kraepelin (1895, 1899). In the absence of a full revision of *Charon* in which the status of each name is fully assessed, our decision to describe three new species may seem premature. However, we believe that Kraepelin's decision was categorically incorrect and believe that several quite distinct species exist amongst the material examined by him. Evidence for this comes from the examination of much Indonesian and New Guinean material lodged in WAM, and the holotype male of *C. grayi* lodged in BMNH and a syntype female of *C. beccarii* Thorell lodged in SMNH, none of which is conspecific with any of the species named below. Indeed, the syntype of *C. beccarii* possesses a basitibia III which is clearly subdivided, unlike any other *Charon* species examined by us, which we suspect is evidence of specific status of this species. Whether the apparently sympatric *C. subterraneus* possesses a similar pattern we are not sure. However, we do not formally remove *C. hoeveni*, *C. beccarii*, *C. subterraneus* and *C. papuanus* from the synonymy with *C. grayi* until the necessary revisionary work on the southeast Asian fauna has been completed. Our decision to describe the Australian species as new is further based upon their obvious distinctiveness from each other, making it less likely that they are in fact conspecific with any of the names previously proposed in the literature.

Charon oenpelli new species
(Figs. 1–6, 17, 18; Table 1)

Types.—Holotype male from sandstone caves near Oenpelli Reservoir, ca. 9 km S of Oenpelli, Northern Territory, Australia (12°23′58″S, 133°05′09″E), 3 May 1994 (G.R. Brown, P.G. Horner, G. Husband) (NTM). Paratypes: 2♀, same data (NTM); 1♂1♀, same data (WAM 96/1602–1603); 2♀, same data except, 4 October 1993 (D.N. Wilson,
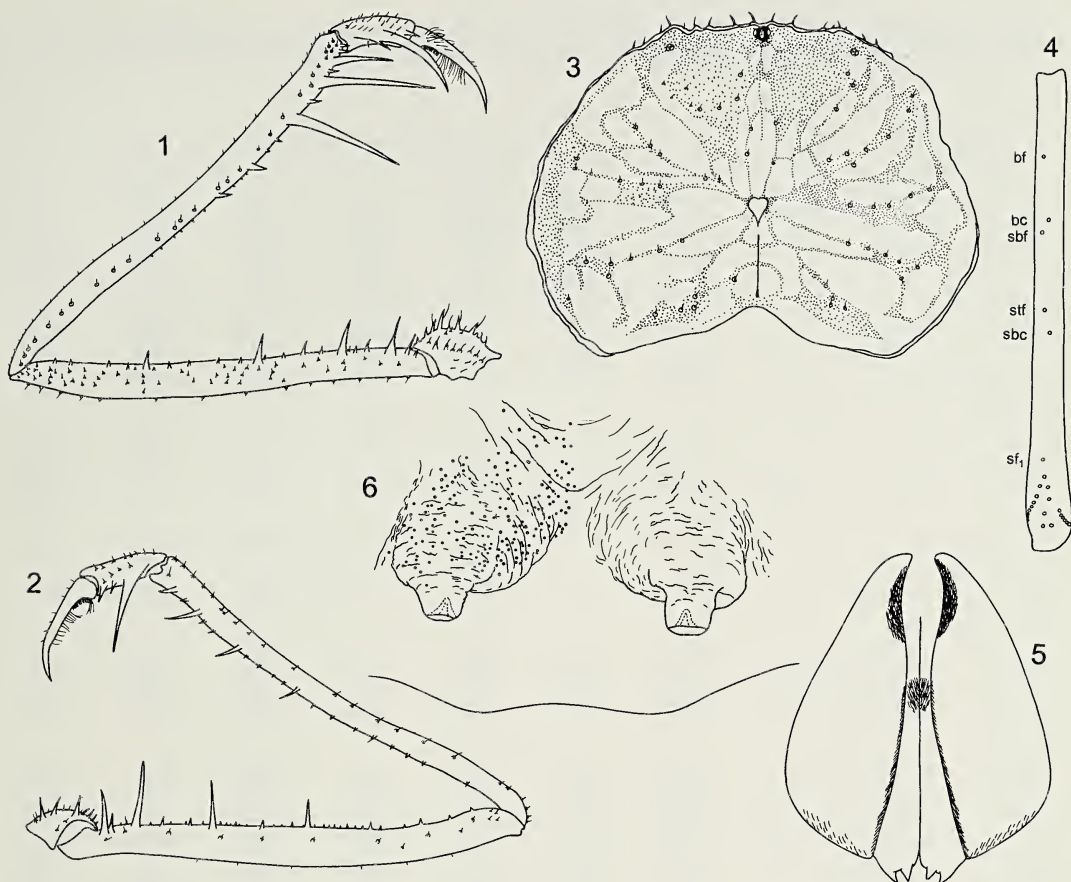
Figures 1–6.—*Charon oenpelli* new species, male holotype (unless otherwise stated). 1, Left pedipalp, dorsal; 2, Left pedipalp, ventral; 3, Carapace; 4, Left distitibia IV; 5, Male genitalia, dorsal; 6, Female paratype, genitalia, dorsal (pores omitted on one side).

G.A. Husband) (NTM); 2♂, same data except, 30 November 1996 (G.R. Brown) (NTM); 1♂ from sandstone caves near Gunbiyarrmi, near Oenpelli [12°23′18″S, 133°05′09″E, 9 May 1992 (I. Morris) (NTM); 1♂, same data except, 30 August 1992 (J. Webber, I. Morris & G.R. Brown) (NTM).

Other material.—AUSTRALIA: *Northern Territory:* 1 juv. ♂ from sandstone caves near Oenpelli Reservoir, ca. 9 km S of Oenpelli (12°23′58″S, 133°05′09″E), 3 May 1994 (G.R. Brown, P.G. Horner, G. Husband) (NTM); 1♀ (exuvium), 1 juv. ♀, same data except, 17 July 1996 (G. Husband) (NTM).

Etymology.—The specific epithet is a noun in apposition taken from the region from which the species has been collected.

Diagnosis.—*Charon oenpelli* differs from other species of *Charon* by the following combination of characters: basitibia III with 1 segment; basitibia IV with 4 segments; distitibia IV with 26 trichobothria; pedipalps long and slender; eyes reduced in size.

Description.—*Holotype male:* Carapace, pedipalps, leg I and patellae II, III, IV and distitibiae-tarsi II, III, IV all reddish-brown. Tergites and femora II, III, IV more yellowish than carapace. Carapace (Fig. 3): anterior margin straight, with rounded lobe on antero-ventral corners; anterior margin with fine 9 setae between lobes. Sulcus distinct. Median and lateral eyes lightly reduced in size. Median ocular tubercle darker than remainder of carapace, with eyes directed laterally. Carapace with numerous fine tubercles, many with small, acicular setae. Chelicera: hand with 4 teeth on antero-lateral margin, most basal tooth distally incised, 1 proximal tooth on re-

Table 1.—Selection of meristic and spination characters in Australian species of *Charon*.

		Charon oenpelli new species						
		WAM 96/1602 Para-type ♂	NTM Para-type ♂	NTM Holo-type ♂	NTM Para-type ♂	NTM Para-type ♂	NTM Para-type ♂	NTM Juvenile ♂
Carapace	length	5.13	4.69	5.63	4.22	5.00	5.00	3.11
	width	7.50	6.88	8.00	6.06	7.50	7.38	4.26
Median ocular tubercle		0.55	0.48	0.55	0.41	0.50	0.52	0.36
Lateral eyes		2.78	2.48	3.22	2.38	2.81	2.81	1.55
Lateral eye to anterior edge		0.57	0.45	0.48	0.41	0.41	0.48	0.36
Lateral eye to lateral edge		0.43	0.43	0.52	0.31	0.48	0.45	0.29
Genital operculum	length	1.79	1.62	1.67	—	1.90	1.59	0.71
	width	2.74	2.59	3.14	—	3.10	3.15	1.86
Abdomen	length	9.20	8.10	11.60	8.60	8.30	9.00	6.69
	width	5.00	4.88	5.50	4.90	5.30	5.81	3.56
Pedipalp:								
Trochanter	length	2.56	2.07	2.85	1.81	2.20	2.26	1.19
	width	1.56	1.19	1.44	1.19	1.29	1.26	0.81
Femur	length	11.50	8.10	15.10	7.00	10.20	10.50	3.74
	width	1.25	1.07	1.19	0.98	1.20	1.14	0.67
Patella	length	12.56	8.10	15.42	7.38	10.90	11.00	3.44
	width	1.63	0.60	0.88	0.88	0.90	0.83	0.56
Tibia	length	2.80	2.33	3.03	1.92	2.44	2.62	1.41
	width	0.96	0.90	1.00	0.74	0.81	0.83	0.48
Tarsus		3.30	2.70	3.85	2.81	2.70	2.70	1.63
Spines	Trochanter	D6 V8	D5 V8	D6 V7	D6 V5	D6 V6	D6 V6	D5 V10
	Femur	D24 V25	D22 V23	D25 V27	D17 V17	D26 V24	D25 V24	D12 V10
	Patella	D24 V20	D19 V18	D31 V29	D20 V18	D21 V24	D24 V24	D12 V11
	Tibia	D5 V3	D4 V4	D3 V3	D3 V3	D4 V3	D5 V3	D3 V3
Leg I	Femur length	22.90	19.40	24.50	16.85	21.30	20.70	10.90
	Patella length	1.12	1.00	1.10	0.81	0.95	0.95	0.62
	Tibia length	46.11	40.07	50.09	35.46	42.10	43.72	19.34
	Tarsus length	44.52	41.34	48.34	34.82	43.70	42.90	23.00
Leg II	Femur length	12.24	10.40	13.67	9.30	11.45	12.20	6.56
	Patella length	1.50	1.40	1.64	1.28	1.61	1.54	0.95
	Basitibia length	12.72	10.70	13.83	9.20	11.80	12.24	6.38
	Distibia length	5.19	4.60	5.56	4.20	4.80	5.31	3.18
	Metatarsus + tarsus length	3.70	2.31	2.50	2.04	2.40	2.50	1.59

Table 1.—Extended.

NTM Para-type ♀	WAM 96/1603 Para-type ♀	NTM Para-type ♀	NTM Para-type ♀	NTM Para-type ♀	NTM ♀ (exu-vium)	NTM Juvenile ♀	*Charon trebax* new species QM S 105078 Holotype ♀	*Charon gervaisi* new species WAM 96/1601 Holotype ♀	QM S17225 Paratype ♀
4.88	5.00	5.80	6.20	5.31	5.70	2.50	4.69	5.30	5.50
7.44	7.09	8.20	8.65	7.50	7.00	3.75	7.19	8.40	8.80
0.48	0.45	0.59	0.56	0.50	0.571	0.30	0.60	0.74	0.77
2.78	2.80	3.11	3.73	2.92	2.59	1.37	2.78	2.89	3.03
0.52	0.56	0.57	0.60	0.50	0.51	0.11	0.48	0.48	0.38
0.48	0.43	0.48	0.64	0.50	0.51	0.22	0.52	0.71	0.95
1.87	1.63	2.10	—	3.18	—	—	—	1.48	—
3.18	3.14	3.49	—	1.88	—	—	—	3.26	—
8.60	8.82	8.60	12.05	9.90	9.50	4.56	11.30	10.90	8.40
5.38	5.29	5.88	7.84	5.79	5.50	2.22	5.80	6.44	6.50
2.09	2.14	2.58	2.67	2.52	2.00	0.89	2.10	2.60	2.26
1.36	1.24	1.38	0.18	1.50	1.30	0.59	1.41	1.48	1.45
8.60	8.10	9.60	12.88	9.60	7.80	2.85	6.40	7.40	8.50
1.26	1.20	1.33	1.40	1.24	1.20	0.55	1.73	1.38	1.56
8.90	9.80	10.40	14.04	10.00	8.10	2.96	7.30	8.30	8.80
0.95	0.93	1.04	1.00	0.95	0.90	0.48	1.07	1.09	1.48
1.74	2.70	3.00	3.83	2.90	2.00	1.11	2.22	2.43	2.59
0.89	0.86	1.06	1.07	1.00	0.80	0.44	0.98	1.00	1.04
3.15		3.40	4.67	3.66	3.20	1.81	2.74	3.11	3.33
D6 V6	D7 V14	D3 V4	D6 V3	D7 V5	D 6 V	D4 V3	D8 V4	D5 V7	D7 V6
D22 V19	D31 V32	D23 V23	D25 V24	D19 V18	D21	D9 V9	D16 V14	D14 V17	D20 V20
D17 V17	D20 V22	D18 V20	D23 V27	D23 V23	D18	D8 V10	D15 V19	D17 V16	D22 V19
D4 V3	D4 V3	D4 V3	D6 V4	D4 V3	D4	D4 V2	D3 V2	D3 V2	D2 V2
19.50	18.90	21.00	24.77	20.50	18.30	8.50	13.04	18.76	17.01
0.93	1.07	1.12	1.07	1.02	0.93	0.60	0.64	1.26	1.07
37.37	36.90	40.08	48.56	41.70	39.75	17.50	21.50	32.90	29.40
36.57	34.30	38.30	45.41	40.50	37.37	18.60	19.70	37.30	34.98
10.90	11.38	11.50	14.05	12.40	10.80	5.50	7.70	10.20	10.30
1.53	1.57	1.50	1.82	1.48	1.40	0.80	1.31	1.56	1.50
10.95	15.30	10.60	14.86	12.40	10.50	4.60	7.25	9.40	9.30
4.78	4.64	5.15	5.59	5.25	4.20	2.50	3.50	4.38	3.90
2.27	2.24	2.35	2.83	2.44	1.60	1.20	2.07	2.60	2.50

Table 1.—Continued

		Charon oenpelli new species						
		WAM 96/1602 Para- type ♂	NTM Para- type ♂	NTM Holo- type ♂	NTM Para- type ♂	NTM Para- type ♂	NTM Para- type ♂	NTM Juvenile ♂
Leg III	Femur length	13.51	11.00	14.31	10.50	12.20	12.58	7.30
	Patella length	1.67	1.43	1.86	1.38	1.75	1.67	1.00
	Basitibia length	15.19	12.56	16.06	11.70	13.99	14.63	7.50
	Distitibia length	5.40	4.70	5.94	4.56	5.20	5.75	3.48
	Metatarsus + tarsus length	2.89	2.44	3.06	2.19	2.50	2.50	1.70
Leg IV	Femur length	12.10	10.10	13.28	9.80	11.10	11.50	6.88
	Patella length	1.57	1.31	1.57	1.19	1.52	1.50	0.90
	Basitibia length	15.42	12.40	15.90	12.00	14.31	14.63	7.55
	Distitibia length	4.63	4.06	4.77	4.00	4.40	4.40	2.96
	Metatarsus + tarsus length	2.69	2.50	2.85	2.50	2.70	2.50	1.85
No. of segments	Tibia I	25	25	25	35	26	26	25
	Metatarsus I	1	1	1	1	1	1	1
	Tarsus I	44	44	44	48	44	33	44
	Basitibia II	1	1	1	1	1	1	1
	Distitibia II	1	1	1	1	1	1	1
	Metatarsus II	1	1	1	1	1	1	1
	Tarsus II	4	4	4	4	4	4	4
	Basitibia III	1	1	1	1	1	1	1
	Distitibia III	1	1	1	1	1	1	1
	Metatarsus III	1	1	1	1	1	1	1
	Tarsus III	4	4	4	4	4	4	4
	Basitibia IV	4	4	4	4	4	4	4
	Distitibia IV	1	1	1	1	1	1	1
	Metatarsus IV	1	1	1	1	1	1	1
	Tarsus IV	4	4	4	4	4	4	4

tro-lateral margin. Movable finger with 6 small basal teeth. Pedipalps (Figs. 1, 2): long and slender (Figs. 17, 18). Trochanter with 6 spines on antero-dorsal margin, 4 spines on antero-ventral margin, and 7 spines on latero-ventral margin. Femur with 4 major spines and 21 smaller spines on antero-dorsal mar-gin; major spine I the longest, with the others decreasing distally (I > II > III > IV); antero-ventral margin with 4 major spines and 23 smaller spines, major spine II the longest, with others arranged II > III > I > IV. Patella with 4 major spines and 27 smaller spines on an-tero-dorsal margin; major spine II the longest,

Table 1.—Extended (continued).

NTM Para-type ♀	WAM 96/1603 Para-type ♀	NTM Para-type ♀	NTM Para-type ♀	NTM Para-type ♀	NTM ♀ (exu-vium)	NTM Juvenile ♀	*Charon trebax* new species QM S 105078 Holotype ♀	*Charon gervaisi* new species WAM 96/1601 Holotype ♀	*Charon gervaisi* new species QM S17225 Paratype ♀
12.40	12.45	12.50	15.05	12.56	11.60	6.20	8.50	11.00	10.80
1.55	1.63	1.70	1.98	2.22	1.60	1.20	1.38	1.50	1.60
13.67	14.88	14.00	17.21	14.47	12.20	5.70	8.10	11.00	10.90
4.88	5.06	5.50	6.42	5.31	4.50	2.80	3.50	4.50	4.20
2.60	2.66	2.80	2.82	2.94	2.00	1.50	2.30	2.00	3.00
10.80	10.98	11.30	11.46	12.40	10.50	5.50	7.60	10.40	10.30
1.46	1.62	1.70	1.92	1.78	1.40	0.80	1.36	1.55	1.50
13.45	14.60	16.22	16.47	13.51	12.00	6.10	8.30	11.00	11.80
4.13	4.39	4.40	5.34	4.44	3.90	2.50	3.00	4.40	3.50
2.67	2.66	3.10	2.93	2.81	2.10	1.50	2.21	3.00	3.00
25	26	26	25	25	27	—			
1	1	1	1	1	1	—			
44	43	43	44	44	44	—	25	26	26
1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	44	44	47
1	1	1	1	1	1	1	1	1	1
4	4	4	4	4	4	4	1	1	1
1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	4	4	4
1	1	1	1	1	1	1	1	1	1
							1	1	1
4	4	4	4	4	4	4	1	1	1
4	4	4	4	4	4	4	4	4	4
1	1	1	1	1	1	1	3	4	4
1	1	1	1	1	1	1	1	1	1
							1	1	1
4	4	4	4	4	4	4	4	4	4

with others arranged II > III > IV > I; antero-ventral margin with 5 major spines and 24 smaller spines, major spine III the longest, with others arranged III > II > I; mt IV > V. Tibia with 3 spines on the antero-dorsal margin, with I being the longest, with others similar size; antero-ventral margin with 3 spines, arranged I > III > II. Tarsus without spines, not divided. Legs: leg I with 25 tibial and 44 tarsal segments. Basitibia II and III with 1 segment. Basitibia IV with 4 segments; first 3 without trichobothria, fourth segment with 1 trichobothrium (0.39). Distitibia IV with 26 trichobothria (Fig. 4): bf (0.17), bc (0.32), sbf

(0.35), stf (0.50), sbc (0.55), sf$_1$ (0.80). Tarsi
II, III and IV with 4 segments. Sternum: tri-
partite; anterior section only slightly expanded
basally. Genitalia: with paired, posteriorly di-
rected projections (Fig. 5).

Paratype female: (NTM). Carapace, pedi-
palps, leg I, patellae II, III, IV, basitibia-tarsus
II, III, IV all reddish-brown. Abdomen and
femora II, III, IV are a lighter orange-brown.
Carapace: anterior margin straight, with 9 fine
setae. Sulcus distinct surrounded by raised ar-
eas on carapace separated by radiating sulci.
Median and lateral eyes lightly reduced in
size. Median ocular tubercle darker than re-
mainder of carapace, with eyes directed lat-
erally. Carapace with numerous fine tubercles,
many with small, acicular setae. Chelicera:
hand with 4 teeth on antero-lateral margin,
most basal tooth distally incised, 1 proximal
tooth on retro-lateral margin. Movable finger
with 6 small basal teeth. Pedipalps: long and
slender (Figs. 17, 18). Trochanter with 6
spines on antero-dorsal margin, 9 spines on
antero-ventral margin, and 3 spines on latero-
ventral margin. Femur with 7 major spines
and 18 smaller spines on antero-dorsal mar-
gin, major spine I the longest with others ar-
ranged II > VII > III > VI > V > IV; antero-
ventral margin with 6 major spines and 18
smaller spines; major spine VI longest, with
others arranged I > III > V > II > IV. Patella
with 10 major spines and 13 smaller spines on
antero-dorsal margin; major spine VIII the
longest with others arranged V > III > IX >
II > X> VII > VI > IV > I; antero-ventral
margin with 5 major spines and 22 smaller
spines, major spine IV the longest with others
arranged III > II > I > V. Tibia with 2 major
spines on antero-dorsal margin, with spine I
the largest; antero-ventral margin with 4
spines, arranged I > IV > III > II. Tarsus
without spines, not divided. Legs: leg I with
26 tibial and 44 tarsal segments. Basitibia II
and III with 1 segment. Basitibia IV with 4
segments; first three without trichobothria,
fourth segment with 1 trichobothrium (0.26).
Distitibia IV with 26 trichobothria: bf (0.14),
bc (0.25), sbf (0.30), stf (0.50), sbc (0.60), sf$_1$
(0.80). Tarsi II, III and IV with 4 segments.
Sternum: tripartite; anterior section only
slightly expanded basally. Genitalia (Fig. 6):
gonopods simple, covered with numerous
small pores, distally invaginated; posterior

margin of sternite I sinuate; sternite II with
ventral sac covers.

Remarks.—*Charon oenpelli* has only been
found in sandstone caverns situated near Oen-
pelli, Arnhem Land, and possesses some trog-
lophilic tendencies such as attenuate pedi-
palps, reduced median and lateral eyes, and
pale coloration (Morris (1996), published a
photograph of this species). These caves are
also inhabited by a recently described scor-
pion, *Liocheles extensa* Locket, which also
occurs outside of the cave systems in nearby
woodland (Locket 1995, 1997).

<center>

***Charon trebax* new species**
(Figs. 7–11, 17, 18; Table 1)

</center>

Types.—Holotype female from Cromarty,
Emmett Creek, Queensland, Australia,
19°28'S, 147°03'E, found under rock, near dirt
road going "off to right" between Emmett
and McKenzie Creeks, 31 July 1990 (J. & L.
Ferguson) (QM S105078).

Etymology.—The occurrence of this spe-
cies in the Townsville region has been known
for some time (G.B. Monteith pers. comm.),
but specimens have previously not been cap-
tured. This elusiveness is reflected in the spe-
cific epithet (*trebax* Latin, cunning, crafty).

Diagnosis.—*Charon trebax* differs from
other species of *Charon* by the following
combination of characters: basitibia III with 1
segment; basitibia IV with 3 segments; disti-
tibia IV with 20 trichobothria.

This species is easily distinguished from
other *Charon* species by several character
states, including the presence of only 3 seg-
ments in basitibia IV and only 20 trichoboth-
ria on distitibia IV (Fig. 10).

Description.—*Holotype female:* Carapace
brownish-orange. Pedipalps reddish-brown.
Leg I, patellae-tarsi II, III, IV and abdomen
brownish-yellow. Femora II, III, IV with 4
brown bands and 3 yellow bands. Carapace
(Fig. 9): anterior margin straight, with 9 fine
setae. Sulcus distinct surrounded by raised ar-
eas on carapace separated by radiating sulci.
Median and lateral eyes well-developed. Me-
dian ocular tubercle darker than remainder of
carapace, with eyes directed laterally. Cara-
pace with numerous fine tubercles, many with
small, acicular setae. Chelicera: hand with 4
teeth on antero-lateral margin, most basal
tooth distally incised, 1 proximal tooth on re-
tro-lateral margin. Movable finger with 4
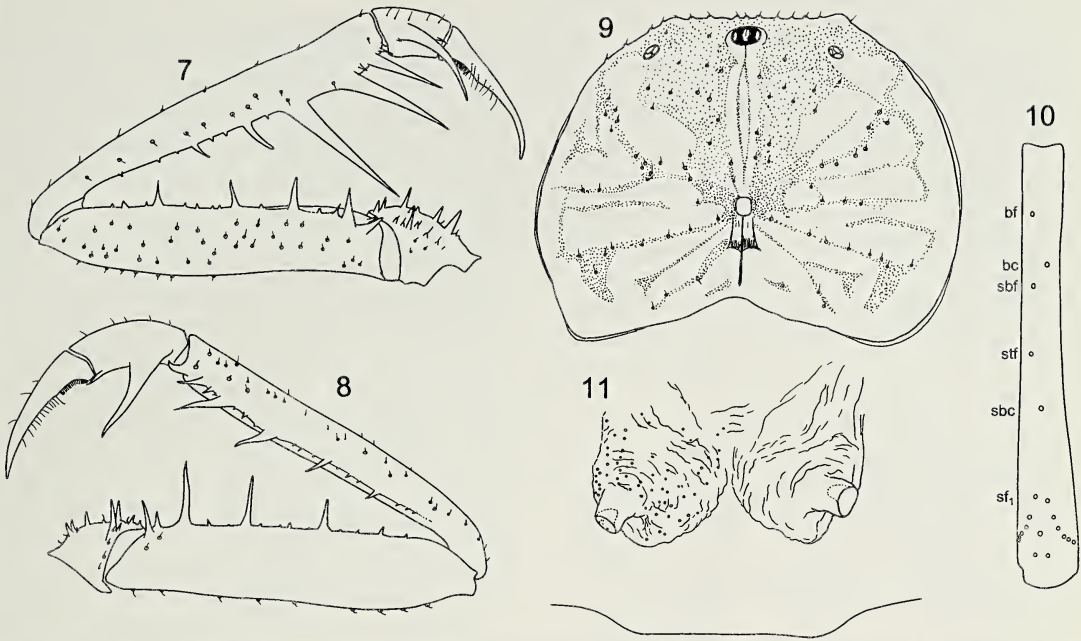
Figures 7–11.—***Charon trebax*** new species, female holotype. 7, Left pedipalp, dorsal; 8, Left pedipalp, ventral; 9, Carapace; 10, Left distitibia IV; 11, Genitalia, dorsal (pores omitted on one side).

small basal teeth. Pedipalps (Figs. 7-8): moderately stout (Figs. 17, 18). Trochanter with 8 spines on antero-dorsal margin, 4 spines on antero-ventral margin, and 4 spines on latero-ventral margin. Femur with 5 major spines and 11 smaller spines on antero-dorsal margin, major spine II the longest with others arranged III > VI > I > V; antero-ventral margin with 4 major spines and 10 smaller spines; major spine II longest, with others arranged III > V > I. Patella with 6 major spines and 9 smaller spines on antero-dorsal margin; major spine III the longest with others arranged IV > V > II > VI > I; antero-ventral margin with 6 major spines and 13 smaller spines, major spine IV the longest with others arranged III > II > VI > VI > I. Tibia with 3 major spines on antero-dorsal margin, with spine I the largest and spines II and III of the same length; antero-ventral margin with 2 spines, with spine I the largest. Tarsus without spines, not divided. Legs: leg I with 25 tibial and 44 tarsal segments. Basitibia II and III with 1 segment. Basitibia IV with 3 segments; first two without trichobothria, third segment with 1 trichobothrium (0.50). Distitibia IV with 20 trichobothria (Fig. 10): bf (0.16), bc (0.27), sbf (0.32), stf (0.47), sbc (0.59), sf_1 (0.79). Tarsi II, III and IV with 4 segments.

Sternum: tripartite; anterior section only slightly expanded basally. Genitalia (Fig. 11): gonopods simple, covered with few small pores, distally invaginated; posterior margin of sternite I sinuate; sternite II with ventral sac covers.

Remarks.—*Charon trebax* is only known from a single locality near Townsville, Queensland.

Charon gervaisi new species
(Figs. 12–18; Table 1)

Types.—Holotype female from Boat Club, Settlement, Christmas Island, Australia [10°25'S, 105°40'E], in wood pile, 10 February 1991 (H. Yorkstan) (WAM 96/1601). Paratype: 1♀ from Christmas Island, 28 February-6 March 1980 (J. Covacevich, H. Heatwole) (QM S17225).

Etymology.—This species is named for Paul Gervais who described the first species attributed to the genus *Charon*.

Diagnosis.—*Charon gervaisi* differs from other species of *Charon* by the following combination of characters: basitibia III with 1 segment; basitibia IV with 4 segments; distitibia IV with 30 trichobothria, including an extra sbf trichobothrium; carapace with very
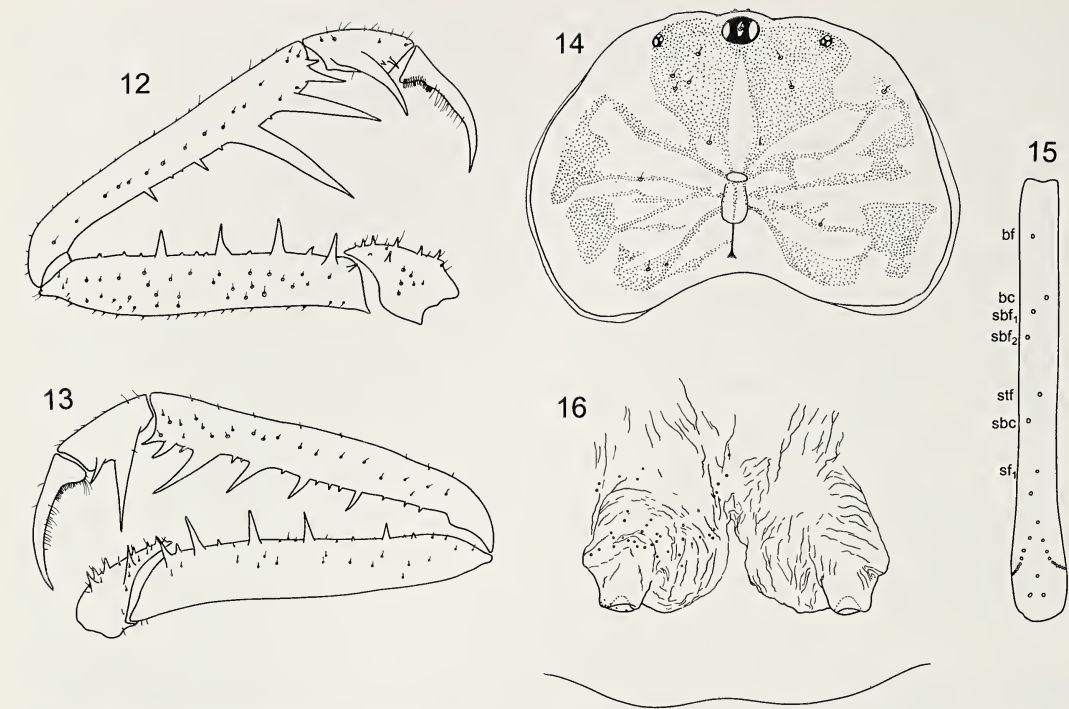
Figures 12–16.—*Charon gervaisi* new species, female holotype. 12, Left pedipalp, dorsal; 13, Left pedipalp, ventral; 14, Carapace; 15, Left distitibia IV; 16, Genitalia, dorsal (pores omitted on one side).

few seta-bearing tubercles; female gonopods with very few pores.

The extra trichobothrium in the sbf series (Fig. 15) is a diagnostic feature of this species, and is found in both legs in both of the specimens listed above. Numerous other characters such as the reduced number of seta bearing tubercles on the carapace and the reduced

number of pores on the female gonopods are also diagnostic.

Description.—*Holotype female:* Pedipalps: trochanter dark brown. Tibia and tarsus dark reddish-brown. Patella and femur brown and orange bands. Chelicera dark reddish-brown. Carapace, leg I and patellae II, III and IV reddish-brown. Abdomen, basitibia-tarsus II, III,
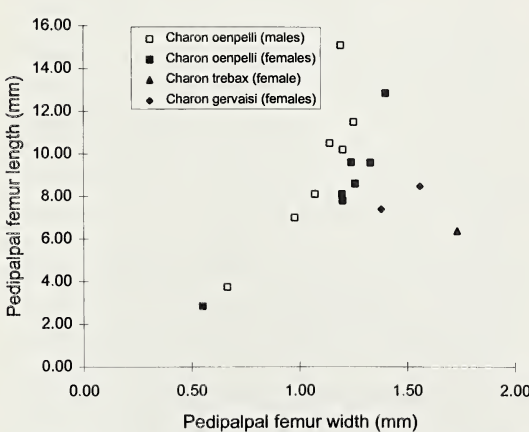
Figure 17.—Pedipalpal femur length vs. width in three Australian species of *Charon*.
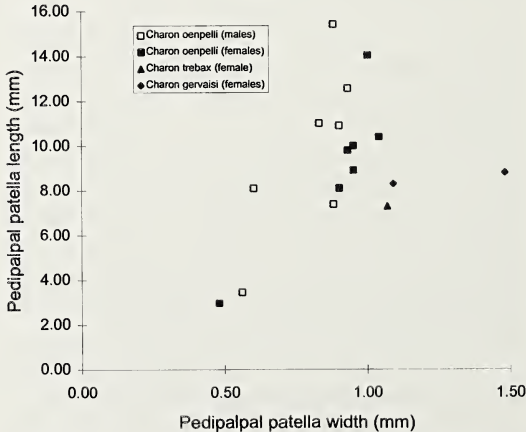
Figure 18.—Pedipalpal patella length vs. width in three Australian species of *Charon*.

IV and IV light brown. Femora II, III and IV with 4 brown bands and 3 yellow bands. Carapace (Fig. 14): anterior margin straight with a medial lobe, with 9 fine setae. Sulcus distinct surrounded by raised areas on carapace separated by radiating sulci. Median and lateral eyes well-developed. Median ocular tubercle darker than remainder of carapace, with eyes directed laterally. Carapace with numerous fine tubercles, but only some with small, acicular setae. Chelicera: hand with 4 teeth on antero-lateral margin, most basal tooth distally incised, 1 proximal tooth on retro-lateral margin. Movable finger with 6 small basal teeth. Pedipalps (Figs. 12, 13): moderately stout (Figs. 17, 18). Trochanter with 5 spines on antero-dorsal margin, 7 spines on antero-ventral margin, and 3 spines on latero-ventral margin. Femur with 4 major spines and 10 smaller spines on antero-dorsal margin, major spine II the longest with others arranged I > III > IV; antero-ventral margin with 5 major spines and 12 smaller spines; major spine II longest, with others arranged III > IV > I > V. Patella with 6 major spines and 11 smaller spines on antero-dorsal margin; major spine III the longest with others arranged IV > V > II > VI > I; antero-ventral margin with 6 major spines and 10 smaller spines, major spine IV the longest with others arranged III > II > I > V > VI. Tibia with 3 major spines on antero-dorsal margin, with spine I the largest and spines II and III of the same length; antero-ventral margin with 2 spines, with spine I the largest. Tarsus without spines, not divided. Legs: leg I with 26 tibial and 44 tarsal segments. Basitibia II and with 1 segment. Basitibia IV with 4 segments; first three without trichobothria, fourth segment with 1 trichobothrium (0.37). Distitibia IV with 30 trichobothria (Fig. 15): bf (0.13), bc (0.27), sbf_1 (0.30), sbf_2 (0.36), sbc (0.49), stf (0.55), sc_1 (0.66). Tarsi II, III and IV with 4 segments. Sternum: tripartite; anterior section only slightly expanded basally. Genitalia (Fig. 16): gonopods simple, covered with few small pores, distally invaginated; posterior margin of sternite I sinuate; sternite II with ventral sac covers.

Remarks.—*Charon gervaisi* is presently known only from Christmas Island, although an Indonesian origin for the species is very likely, given that Christmas Island lies only some 360 km off the south coast of Java.

ACKNOWLEDGMENTS

LITERATURE CITED

Butler, A.G. 1873. A monographic revision of the genus *Phrynus,* with descriptions of four remarkable new species. Ann. Mag. Nat. Hist., (4)12: 17–125.

Gervais, P. 1842. Entomologie. L'Institut, J. Universal Sci. Soc. Savantes France l'Étranger, 1ere Section, 10:76.

Gervais, P. 1844. Aptéres, *In* Histoire naturelle des Insectes. (C.A. Walckenaer), Vol. 3, Librairie Encyclop. de Roret, Paris.

Gravely, F.H. 1915. A revision of the Oriental subfamilies of Tarantulidae. Rec. Indian Mus., 11: 433–455.

Harvey, M.S. 1985. Amblypygi. Pp. 156–157, *In* Zoological Catalogue of Australia, vol. 3. (D.W. Walton, ed.). Australian Gov. Publ. Serv., Canberra.

Harvey, M.S. 1992. The phylogeny and classification of the Pseudoscorpionida (Chelicerata: Arachnida). Invert. Taxon., 6:1373–1435.

Hoeven, J. van der. 1842. Bijdragen tot de Kennis van het geslacht *Phrynus* Oliv. Tidj. Natuur. Ges. Physiol., 9:68–93.

Karsch, F. 1879. Ueber eine neue Eintheilung der Tarantuliden (Phrynidae aut.). Arch. Naturg., 45: 189–197.

Karsch, F. 1880. Zur Kenntniss der Tarantuliden. Arch. Naturg., 46:244–249.

Kraepelin, K. 1895. Revision der Tarantuliden Fabr. (Phryniden (Latr.)). Verhandl. Naturhist. Ver. Hamburg, 13(3):3–53.

Kraepelin, K. 1899. Scorpiones und Pedipalpi. Tierreich, 8:i–xviii, 1–265.

Lauterer, J. 1895. An undescribed species of *Charon,* with notes on the metamorphosis of the first pair of ambulatory legs into a physiological pair of feelers. Report of the Sixth Meeting of the Australasian Asso. Advanc. Sci., pp. 413–414.

Locket, N.A. 1995. A new ischnurid scorpion from the Northern Territory, Australia. Rec. Western Australian Mus., Suppl., 52:191–198.

Locket, N.A. 1997. *Liocheles extensa,* a replacement name for *Liocheles longimanus* Locket,

1995 (Scorpiones: Ischnuridae). Rec. Western Australian Mus., 18:331.

Mello-Leitão, C. 1931. Pedipalpos do Brasil e algumas notas sobre a ordem. Arch. Museu Nacional, 33:7–72.

Monteith, G.B. 1965. Notes on the order Amblypygi (Arachnida) in Australia. J. Entomol. Soc. Queensland, 4:87.

Mullinex, C.L. 1975. Revision of *Paraphrynus* Moreno (Amblypygida: Phrynidae) for North America and the Antilles. Occ. Pap. California Acad. Sci., 116:1–80.

Morris, I. 1996. Steve Parish Natural History Guide. Kakadu National Park, Australia. Pp. 224, Steve Parish Publ., Fortitude Valley.

Quintero, D. 1981. The amblypygid genus *Phrynus* in the Americas (Amblypygi, Phrynidae). J. Arachnol., 9:117–166.

Quintero, D. 1986. Revision de la clasificacion de Amblypygidos pulvinados: creacion de subordenes, una nueva familia y un nuevo genero con tres nuevas especies (Arachnida: Amblypygi). Pp. 203–212, *In* Proc. Ninth Intern. Cong. Arachnol., Panama 1983. (W.G. Eberhard, Y.D. Lubin & B.C. Robinson, eds.). Smithsonian Institution, Washington, D.C.

Shear, W.A., P.A. Selden, W.D.I. Rolfe, P.M. Bonamo & J.D. Grierson. 1987. New terrestrial arachnids from the Devonian of Gilboa, New York (Arachnida, Trigonotarbida). American Mus. Novit., 2901:1–74.

Shultz, J.W. 1989. Morphology of locomotor appendages in Arachnida: Evolutionary trends and phylogenetic implications. Zool. J. Linn. Soc., 97:1–56.

Simon, E. 1892. Arachnides des îles Philippines. Ann. Soc. Entomol. France, 61:35–52.

Snodgrass, R.E. 1948. The feeding organs of Arachnida, including mites and ticks. Smithson. Misc. Coll., 110(10):1–93.

Thorell, T. 1888. Pedipalpi et scorpioni dell'Arcipelago Malese conservati nel Museo Civico di Storia Naturale di Genova. Ann. Mus. Civ. Stor. Nat. Genova, (2)6:327–428.

Thorell, T. 1889. Aracnidi Artrogastri Birmani raccolti da L. Fea nel 1885-1887. Ann. Mus. Civ. Stor. Nat. Genova, (2)7:521–729.

Webber, J. 1992. The first record of an amblypygid from the Northern Territory. Australasian Arachnol., 45:6.

Weygoldt, P. 1996. Evolutionary morphology of whip spiders: towards a phylogenetic system (Chelicerata: Arachnida: Amblypygi). J. Zool. Syst. Evol. Research, 34:185–202.

A NEW TROGLOBITIC SCORPION OF
THE GENUS *TYPHLOCHACTAS* (SUPERSTITIONIDAE)
FROM VERACRUZ, MEXICO

W. David Sissom: Department of Life, Earth and Environmental Sciences, West Texas A & M University, Box 60808, Canyon, Texas 79016 USA

James C. Cokendolpher: 2007 29th Street, Lubbock, Texas 79411 USA

ABSTRACT. A distinctive new troglobitic scorpion of the genus *Typhlochactas* Mitchell from Sótano de Poncho near Municipio Tlaquilpa, Veracruz, Mexico is described and compared to the other members of the genus from the eastern ranges of the Sierra Madre Oriental.

The genera *Superstitionia* Stahnke 1940, *Typhlochactas* Mitchell 1968, *Sotanochactas* Francke 1986, and *Alacran* Francke 1982 comprise what is thought to be a compact monophyletic group. Francke (1982) considered these genera to represent the subfamily Superstitioninae Stahnke 1940, placed *incertae sedis* in the "Chactoidea" (= Chactidae Laurie 1896 + Vaejovidae Thorell 1876 + Iuridae Thorell 1876). Subsequently, he placed it in the Chactidae (Francke 1985), and that status was retained by Sissom (1988, 1990). Stockwell (1992) elevated this subfamily to the familial level and suggested a closer relationship to the Vaejovidae and Iuridae than to the Chactidae. He also added two additional genera, the endogean *Belisarius* Simon 1879 from the Pyrenees Mountains in France and Spain and the troglobitic *Troglotayosicus* Lourenço 1981 from Ecuador, into the Superstitionidae without evidence of "definitive association". While we tentatively agree with the recognition of the Superstitionidae as a valid family (on the basis of Francke's 1982 diagnosis of the subfamily), we express reservations on the inclusion of *Belisarius* and *Troglotayosicus* into the family without firm evidence.

The genus *Typhlochactas* consists of five species in eastern and southern Mexico (Mitchell 1968; Mitchell & Peck 1977; Francke 1986; Sissom 1988). Three of these species (*T. rhodesi* Mitchell 1968, *T. reddelli* Mitchell 1968, and *T. cavicola* Francke 1986) are troglobites, and two (*T. sylvestris* Mitchell & Peck 1977 and *T. mitchelli* Sissom 1988)

are known from forest litter in the mountains of Oaxaca. All are small, eyeless forms with greatly reduced pigmentation. It is the purpose here to describe another troglobitic species of this genus that was recently collected from a cave in northeastern Veracruz, Mexico.

With the transfer of *T. elliotti* Mitchell 1971 into the genus *Sotanochactas* by Francke (1982) and inclusion of several new species since that time, the diagnosis for the genus requires emendation. Francke's (1982) diagnosis for the subfamily Superstitioninae will serve as a proper diagnosis for the family Superstitionidae. The two tribes, Superstitionini and Typhlochactini, should be elevated to subfamilies and may also be diagnosed by Francke's characters.

Typhlochactas Mitchell 1968

Typhlochactas Mitchell 1968: 754–756 (original description); Mitchell 1971: 238 (part); Vachon 1974: 914, 923; Soleglad 1976: 253–254; Mitchell & Peck 1977: 164–165 (part; revised diagnosis); Francke 1985: 14, 16, 20; Francke 1986: 8; Sissom 1900: 109, 114; Stockwell 1992: 410, 412 (key), 419, fig. 3, 28, 30, 33, 35.
Typlochactas (sic): Díaz Najera 1975: 3.

Diagnosis.—Typhlochactinae with color pale yellowish to whitish; sclerotization weak; caudal segments with carination reduced; cheliceral fixed finger with two basalmost teeth either separate or forming a bicusp; cheliceral movable finger with either three, four, or five dorsal teeth; prolateral pedal spurs present or absent; tarsi armed ventrally with two submedian, somewhat irregular rows of setose bristles; pedipalp patella with tricho-

bothrium v_2 displaced to external face; pedipalp chela fixed finger about as long as or slightly longer than chela palm; chela trichobothria as follows: *ib* and *it* situated near base of fixed finger, *eb* (basalmost of the external series) at extreme base of finger; pedipalp chela fixed finger with four to seven oblique rows of denticles along cutting margin.

Type species.—By subsequent designation (Mitchell & Peck 1977) *Typhlochactas rhodesi* Mitchell 1968.

Typhlochactas granulosus new species
(Figs. 1–11)

Type data.—Holotype male taken from Sótano de Poncho, Municipio Tlaquilpa, Veracruz, Mexico on 22 March 1995 by P. Sprouse; deposited in the American Museum of Natural History, New York.

Etymology.—The specific epithet is derived from the Latin *granum* (meaning "small grain") with the suffix *-osus* (meaning "full of") and refers to the stronger granulation of this species in comparison to its congeners.

Distribution.—Known only from the type locality.

Diagnosis.—Adult male 17.3 mm long. Carapace, tergites, and metasoma sparsely to moderately finely granular; pedipalpal segments, particularly the chela, moderately coarsely granular. Metasomal segment V 1.29 times longer than carapace and about 3.53 times longer than wide. Cheliceral fixed finger with four teeth; basal and medial teeth combined into a compound tooth. Movable finger with four dorsal teeth. Pedipalp chela relatively slender with movable length/chela width ratio 3.05; both chela fingers distinctly longer than carapace; fixed finger of chela with seven slightly oblique rows of granules on dentate margin, with basalmost row shortest; movable finger with seven rows. Legs without pedal spurs; ventral aspect of tarsomere II lacking median row of fine spinules.

Typhlochactas granulosus is most similar to *T. rhodesi* and *T. reddelli*. Both *T. rhodesi* and *T. reddelli* are known only from females, but *T. granulosus* is readily distinguished from them on the basis of several nonsexual characters. *Typhlochactas granulosus* differs from *T. rhodesi* by having seven granular rows on both pedipalpal chela fingers (rather than six rows on each), by having a distinct basal bicusp on the cheliceral fixed finger (not

with the basal teeth separate), and by having only four teeth on the cheliceral movable finger (rather than five).

The species may be distinguished from *T. reddelli* by having seven granular rows on the pedipalpal chela fixed finger (rather than six), with the apical row short (rather than long); by having four teeth on the cheliceral movable finger (rather than five); and by lacking pedal spurs. Additional comparisons of *T. granulosus* with these and other *Typhlochactas* appear in Table 1.

Description.—Based on adult male (Fig. 1), the only known specimen.

Coloration: Body uniformly very pale yellow brown. Legs and proximal pedipalpal segments paler than body; pectines whitish. Dentate margins of pedipalp fingers, cheliceral teeth, and aculeus brownish.

Prosoma: Carapace subquadrate; length equal to posterior width. Surface evenly, finely granular with a few small setae. Anterior margin straight with subtle rounded medial projection. Median longitudinal furrow present, shallow. Median and lateral eyes absent. Sternum as in Fig. 2, with anterior width slightly greater than median length; anterior margin gently convex, posterior margin concave, lateral margins diverging distally; small posteromedial depression present; with two pairs of setae.

Mesosoma: Tergites I–VII, acarinate; pretergites smooth, post-tergites densely, finely granular. Genital operculum (Fig. 2) subelliptical, completely divided longitudinally; genital papillae present. Pectines (Fig. 2) with 5/4 teeth; each with two marginal lamellae and one middle lamella; distal fourth of each pectinal tooth with conspicuous, dense, peg sensillae. Sternites III–VII feebly punctate, sparsely setose; stigmata small, elliptical.

Metasoma: Segment I slightly wider than long, II and III distinctly longer than wide, segment V 3.53 times longer than wide. Segments I–IV: Essentially acarinate, but with dorsolateral areas feebly elevated and granular. Dorsal and lateral surfaces with moderately dense, fine granulation; ventral surfaces of I–III smooth and of IV sparsely granular. Setation of first four segments as follows (setal pairs): dorsolateral setae, 1:1:1:1; lateral setae, 1:1:1:2; ventrolateral setae, 1:2:2:2; ventral submedian setae, 2:2:2/3:3. Segment V 1.29 times longer than carapace; carinae indistinct,

Table 1.—Summary of morphological and morphometric differences in the six species of *Typhlochactas*. Morphometric comparisons of *T. granulosus* with *T. rhodesi* and *T. reddelli* should be interpreted with caution, as the latter are known only from females. Morphometric ratios are calculated from original sources; those given for *T. mitchelli* represent the average of the holotype and paratype males. Abbreviations are as follows: *cav* = *T. cavicola*, *gra* = *T. granulosus*, *red* = *T. reddelli*, *rho* = *T. rhodesi*, *syl* = *T. sylvestris*, *mit* = *T. mitchelli*, L = length, W = width, M = male, F = female. Note: Mitchell (1968) and Mitchell and Peck (1977) listed a measurement for femur depth, but this is probably the same as width as reported by other authors; their measurements are indicated by "*".

Character	cav (M)	gra (M)	red (F)	rho (F)	syl (F)	mit (M)
Basal teeth of cheliceral fixed finger fused into bicusp	no	yes	weakly	no	no	no
Number of teeth on cheliceral fixed finger	4	4	4	4	3	3
Number of dorsal teeth on cheliceral movable finger	4	4	5	5	4	3
Number of granular rows on pedipalp chela fixed finger	6	7	6	6	5	4
Number of granular rows on pedipalp chela movable finger	5	7	7	6	6	5
Granulation of pedipalps	minor	extensive	minor	minor	minor	moderate
Prolateral pedal spurs	absent	absent	present	absent	present	present
Metasomal segment II L/W	0.80	1.29	0.89	0.77	0.57	0.75
Metasomal segment V L/W	2.11	3.53	2.58	2.42	1.78	1.84
Pedipalp femur L/W	2.92	3.75	2.76*	3.49*	2.22*	2.46
Pedipalp chela L/W	3.75	4.89	3.78	3.92	3.00	3.06
Chela movable finger L/chela W	2.20	3.05	2.23	2.46	1.64	1.76

but angles separating faces irregularly granular; all surfaces coarsely granular. Paired setae of segment V: 2 dorsolaterals, 3 laterals, 3 ventrolaterals, and 3/4 ventrals. Sum of metasomal I–V lengths 3.66 times greater than carapace length.

Telson: Vesicle flattened dorsally, moderately globose ventrally (vesicle length/depth = 2.00); telson almost as wide as first metasomal segment, wider than segments II–V. Lateral and ventral aspects of vesicle with irregular granulation; moderately setose. Aculeus very slender and gently curved; junction of aculeus and vesicle well-marked.

Figure 1.—Photograph showing dorsal view of holotype male of *Typhlochactas granulosus* new species.

Chelicerae: Fixed finger (Fig. 3) with four teeth (distal, median, and a basal bicusp). Movable finger (Fig. 3) with four teeth: distal internal tooth large, distinctly separated from others; distal external, subdistal, medial, and basal teeth situated close together at midfinger; medial tooth slightly larger than subdistal and basal teeth. Distinct serrula present on ventrodistal half of movable finger. Dense array of long, thin setae present on medial and ventral surfaces of fixed finger; a few longer hairlike setae situated on ventral aspect of movable finger (proximal to serrula).

Pedipalps: Femur (Fig. 4) 3.75 times longer than wide, with carinae essentially obsolete. All surfaces moderately, coarsely granular. Femur orthobothriotaxic, Type C (Vachon 1974). Patella (Figs. 5–7) 3.61 times longer than

Figures 2–7.—External morphology of holotype male of *Typhlochactas granulosus* new species. 2, Ventral aspect of sternum, genital opercula, and pectines; 3, Dorsal aspect of right chelicera; 4, Dorsal aspect of pedipalp femur; 5, Dorsal aspect of pedipalp patella; 6, External aspect of pedipalp patella; 7, Ventral aspect of pedipalp patella.

wide, with carinae essentially obsolete; dorsal, external, and ventral surfaces moderately, coarsely granular; basal tubercle obsolete. Patella orthobothriotaxic, Type C (Vachon 1974); trichobothria d_1 and d_2 short, but pits not distinctly reduced; trichobothrium v_2 located on external aspect (Fig. 6). Chela (Figs. 8–11): manus slightly swollen, with palm

length/chela width ratio of 2.11; ratio of movable finger length/chela width, 3.06. Dorsal marginal, dorsal secondary, digital, and external secondary carinae represented by irregular rows of coarse granules; dorsointernal and ventrointernal carinae represented by series of smaller granules; carinae of ventral surface obscured by dense granulation. Fixed finger
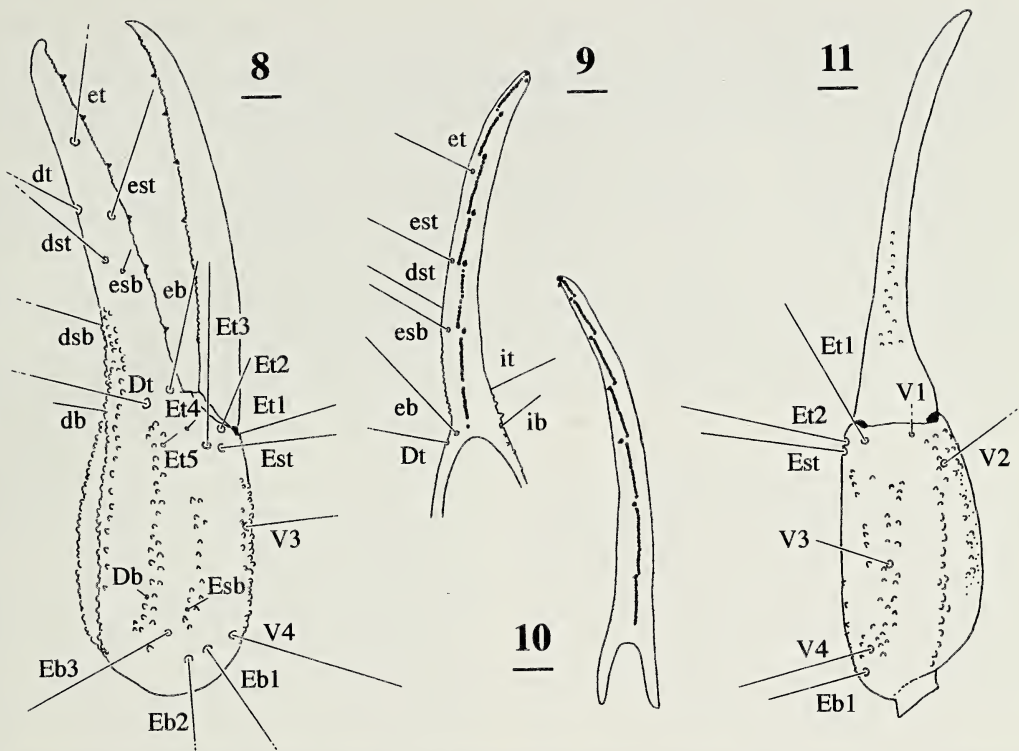
Figures 8–11.—Pedipalp chela morphology of *Typhlochactas granulosus* new species. 8, External aspect of pedipalp chela; 9, Inner margin of pedipalp chela fixed finger, showing placement of trichobothria and dentition; 10, Inner margin of pedipalp chela movable finger, showing dentition; 11, Ventral aspect of pedipalp chela.

(Fig. 9) granular basally along dorsum, with seven slightly oblique rows of denticles from apex to base; basal row shortest; six inner accessory granules, these paired with terminal denticle and enlarged denticles of all but the basalmost row. Movable finger (Fig. 10) with seven slightly oblique rows of denticles; distalmost and basalmost rows shortest; seven inner accessory granules paired with the terminal denticle and enlarged denticles of the denticle rows. Movable finger 1.45 times longer than palm; fixed finger length/carapace length ratio of 1.12. Orthobothriotaxic, Type C (Vachon 1974); trichobothria *ib* and *it* situated just distal to junction of fixed finger and manus (Fig. 9); trichobothria *Db, Esb, Et₄, Et₅, V₁,* and *esb* petite (Fig. 8).

Legs: Tibial and pedal spurs lacking. Ventral aspect of tarsomere II with four or five setae on the prolateral side and four or five on the retrolateral side (irregularly paired); median spinule row absent. Unguis moderately long and curved; dactyl well developed.

Measurements (mm): Total L, 17.30; cara-

pace L, 2.05; mesosoma L, 5.30; metasoma L, 7.50; telson L, 2.45. Metasomal segments: I L/W, 0.95/1.00; II L/W, 1.10/0.85; III L/W, 1.20/0.80; IV L/W, 1.60/0.75; V L/W, 2.65/0.75. Telson: vesicle L/W/D, 1.60/0.95/0.80; aculeus L, 0.85. Pedipalps: femur L/W, 2.25/0.60; patella L/W, 2.35/0.65; chela L/W/D, 4.40/0.90/1.15; fixed finger L, 2.30; movable finger L, 2.75; palm (underhand) L, 1.90.

Comments—In the vial with the holotype was a large, pigmented pedipalp chela that structurally resembles the chela of *Alacran tartarus* Francke 1982, known only from deep caves of the Sistema Huautla, Oaxaca. This chela obviously represents a significant finding, but until more material becomes available it will not be possible to draw comparisons with the Oaxacan specimens. This partial specimen represents the only other scorpion known from the Sotano de Poncho.

According to Peter Sprouse (pers. comm.), Sotano de Poncho is 95 m long and 73 m deep. Mr. Sprouse provides the following description of the cave: "The entrance pit is less

than 2 meters across, but widens as it goes down. This shaft is 53 meters deep, broken by a ledge about halfway down. The talus slope at the bottom leads into a narrow rift to the top of the second drop. This drops 8 meters into a meandering rift. This gradually becomes smaller until it is impassable at a depth of 73 meters. . . The trend of this cave is similar to nearby Sotano del Hombre Miedoso, and could conceivably be related." The holotype of *T. granulosus* was collected on the talus slope at the base of the entrance drop, and the large chela was found in the same area of the cave.

ACKNOWLEDGMENTS

LITERATURE CITED

Díaz Najera, A. 1975. Listas y datos de distribución geográfica de los alacranes de México (Scorpionida). Rev. Inst. Salud. Pública, México, 35:1–36.

Francke, O.F. 1982. Studies on the scorpion subfamilies Superstitioninae and Typhlochactinae, with description of a new genus (Scorpiones, Chactoidea). Assoc. Mexican Cave Stud. Bull., 8:51–61.

Francke, O.F. 1985. Conspectus genericus Scorpionorum, 1758–1982 (Arachnida, Scorpiones).

Occ. Papers Mus., Texas Tech Univ., No. 98, 32 pp.

Francke, O.F. 1986. A new genus and a new species of troglobite scorpion from Mexico (Chactoidea, Superstitioninae, Typhlochactini). Texas Mem. Mus., Speleol. Monogr., 1:5–9.

Mitchell, R.W. 1968. *Typhlochactas,* a new genus of eyeless cave scorpion from Mexico (Scorpionida, Chactidae). Ann. Speleol., 23:753–777.

Mitchell, R.W. 1971. *Typhlochactas elliotti,* a new eyeless cave scorpion from Mexico (Scorpionida, Chactidae). Ann. Speleol., 26:135–148.

Mitchell, R.W. & S.B. Peck. 1977. *Typhlochactas sylvestris,* a new eyeless scorpion from montane forest litter in Mexico (Scorpionida, Chactidae, Typhlochactinae). J. Arachnol., 5:159–168.

Sissom, W.D. 1988. *Typhlochactas mitchelli,* a new species of eyeless, montane forest litter scorpion from northeastern Oaxaca, Mexico (Chactidae, Superstitioninae, Typhlochactini). J. Arachnol., 16:365–371.

Sissom, W.D. 1990. Systematics, biogeography, and paleontology. Pp. 64–160. *In* The Biology of Scorpions. (G.A. Polis, ed.), Stanford Univ. Press, Stanford, California.

Soleglad, M.E. 1976. A revision of the scorpion subfamily Megacorminae (Scorpionida: Chactidae). Wasmann J. Biol., 34:251–303.

Stockwell, S.A. 1992. Systematic observations on North American Scorpionida with a key and checklist of the families and genera. J. Med. Entomol., 29:407–422.

Vachon, M. 1974. Étude des caractères utilisés pour classer les familles et les genres de scorpions (Arachnides). Bull. Mus. Nat. Hist. Nat., Paris, 3rd sér., No. 140, Zool., 104:857–958.

A FOSSIL WHIPSCORPION FROM THE LOWER CRETACEOUS OF BRAZIL

Jason A. Dunlop[1]: Department of Earth Sciences, University of Manchester, Manchester M13 9PL, UK

ABSTRACT. A new fossil whipscorpion (Arachnida, Uropygi, Thelyphonida) is described from the Lower Cretaceous (Aptian) of the Crato Member of the Santana Formation, Ceará Province, Brazil. This specimen is the first record of a Mesozoic thelyphonid, but it is too poorly preserved to be assigned to a family with any confidence. It is named *Mesoproctus rowlandi* new genus and species.

Fossil whipscorpions are rare and are currently known only from the Pennsylvanian of Europe and North America (Brauckmann & Koch 1983; Dunlop & Horrocks 1996). These very ancient forms nonetheless resemble living whipscorpions and can even be referred to modern families, making thelyphonids strong candidates for the title of "living fossils". This paper describes the first Cretaceous whipscorpion, which is particularly significant given the rarity of all arachnids during the Mesozoic (Selden 1993). The Cretaceous Santana Formation already boasts insects (Grimaldi & Maisey 1990), solifuges (Selden & Shear 1996) and spiders (P. Selden pers. comm.). This new specimen adds to the terrestrial arthropod fauna from this locality.

METHODS

The new specimen was obtained from the Ulster Museum (UM), No. K28006. The specimen was studied under a stereomicroscope and Fig. 2 was prepared using a camera lucida. Preserved specimens of the extant whipscorpion *Mastigoproctus* Pocock 1894 were examined for comparative purposes in conjunction with Carboniferous fossil whipscorpions from the collections of the British Museum (Natural History) (BMNH). All measurements are given in mm.

Geological setting.—The new fossil comes from the Crato Member of the Santana Formation, NE Brazil which is dated at Lower Cretaceous (Aptian) in age (Maisey 1990),

[1] Current address: Institut für Systematische Zoologie, Museum für Naturkunde der Humboldt-Universität zu Berlin, Invalidenstraße 43, D-10115, Berlin, Germany.

corresponding to about 110 Mya. The geological setting of the Crato Member has been discussed by Maisey (1990) and Martill (1993). The locality is interpreted as a lacustrine deposit with deposition in both the margins and the center of a lake. Evaporitic structures and the types of pollen and macrofossils found indicate an arid, open sabkha-like environment, i.e., a dry salt-flat close to the margins of a lake. Fossils of plants, insects, fish, frogs, pterosaurs and even feathers having been recorded from the Crato Member. Arachnids are also present, including the solifuge, *Cratosolpuga* Selden 1996, undescribed scorpions (Grimaldi & Maisey 1990) and undescribed mygalomorph and araneomorph spiders (P. Selden pers. comm.). Selden & Shear (1996) cited an opilionid as coming from this locality. This citation may refer to another UM specimen seen by the author, which in fact appears to be a long-legged spider, possibly a pholcid.

Morphological interpretation.—The specimen is preserved on a slab about 13 cm × 16 cm as a part only in a finely laminated, yellowish matrix. Small, pale plant fragments are scattered across the slab. The specimen (Figs. 1, 2) stands out from the matrix and is slightly three-dimensional and brown in color with patches of darker mineralization especially evident on the prosoma and legs. These Crato Member arthropods are preserved as a mineral replacement of the original tissues by goethite (iron oxide hydroxide) (Grimaldi & Maisey 1990; Selden & Shear 1996). The preservation is not as good as that documented in Selden & Shear's (1996) solifuges, where details of carapace morphology and setae on the appendages are evident.

Figure 1.—*Mesoproctus rowlandi* new genus and species. A whipscorpion (Arachnida: Thelyphonida) from the Lower Cretaceous Crato Formation of Brazil. Scale = 1 cm.

The specimen is evidently a thelyphonid since it resembles living whipscorpions (e.g., Millot 1949) by possessing large, well developed, subraptorial pedipalps, narrow, elongate legs with divided tarsi and leg I being characteristically antenniform. These tarsal divisions are obscure in the specimen but can be seen in left legs I–II. The characteristic flagellum, or "whip" is not preserved; extensive preparation posterior to the specimen, before its deposition in the museum, failed to locate this structure. The specimen is too large, about 2.5 cm in body length, to belong to the related order Schizomida (micro-whipscorpions) and the pedipalps in this fossil would have articulated in a horizontal plane, whereas they articulate vertically in schizomids (Millot 1949). Both the prosoma and opisthosoma are too elongate for this specimen to belong to the remaining order

with large subraptorial pedipalps, the Amblypygi (whipspiders), wherein the two body somata tend to be rounder.

Though displaying few morphological details, the legs are preserved laterally, and are held in approximately the same position in life (Millot 1949). Legs I are folded back and directed posteriorly. They are also overlain by the posterior legs and since it might be expected that leg I would be drawn back dorsally above the other legs, this suggests that the specimen is essentially a ventral view. Such a condition would occur when the animal foraged to its side. No details of the sternites and coxosternal region can be distinguished. The opisthosoma ends abruptly and does not narrow into a characteristic pygidium (Millot 1949), which suggests that the terminal end of the opisthosoma and its flagellum have been lost.
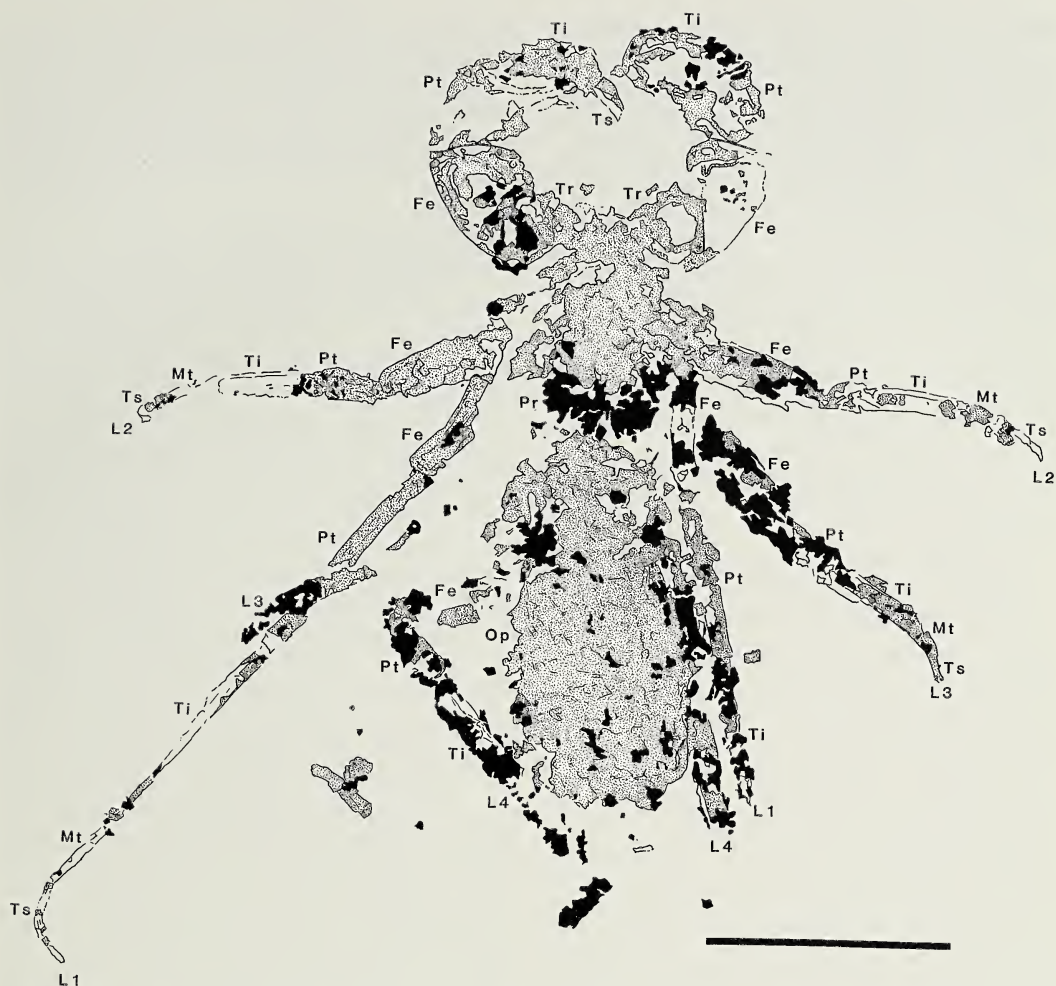
Figure 2.—-Camera lucida drawing of the specimen of *Mesoproctus rowlandi* new genus and species shown in Fig. 1. Pr = prosoma, Op = opisthosoma, Pp = pedipalps, L = leg (with number), Fe = femur, Pt = patella, Ti = tibia, Mt = metatarsus, Ts = tarsus. Black = areas of dark mineralization, stipple = areas of lighter, brown mineralization, white = areas composed of background matrix. Scale = 1 cm.

DISCUSSION

This new specimen is the first record of a Mesozoic whipscorpion. However older, Carboniferous, records are referable to extant families (e.g., Dunlop & Horrocks 1996) and predict their occurrence from the late Palaeozoic to the Recent. The occurrence of this specimen in Brazil is consistent with the distribution of living whipscorpions, which are found in Africa (rarely), eastern and southeastern Asia, North America up to the southern United States, and northeastern South America, including Brazil (Rowland & Cooke 1973). Grimaldi & Maisey (1990) noted a number of xerophilic Crato Member insect

taxa, while Selden & Shear (1996) suggested that their solifuges supported the interpretation of an arid palaeoenvironment. Extant solifuges primarily occur in deserts. Extant whipscorpions are nocturnal predators, typically inhabiting humid, tropical regions, living in leaf litter, under stones or in burrows. However, at least some extant whipscorpions, of which *Mastigoproctus* from the USA is perhaps the best studied, live in arid environments (Crawford & Cloudsley-Thompson 1971), similar to the interpreted environment for the Crato Member. A fossil whipscorpion from an arid palaeoenvironment therefore is not surprising.

Crawford & Cloudsley-Thompson (1971)

noted that *Mastigoproctus* is not physiologically well adapted for desiccation resistance and spends much of its time during dry seasons in deep burrows, only emerging after rain. These authors suggested that whipscorpions are essentially tropical creatures, some of which have become adapted to arid conditions by obtaining moisture from food and by using their sensitive antenniform legs to detect moist, non-horizontal substrates into which they burrow readily and so avoid desiccation. The oldest, Carboniferous, whipscorpions occur in tropical coal swamps. *Mesoproctus* from the more arid Crato Member suggests that this behavioral ability, as opposed to a physiological ability, to avoid desiccation was developed by at least the Lower Cretaceous.

SYSTEMATIC PALAEONTOLOGY

Order Thelyphonida Cambridge 1872

Remarks.—I follow Shultz (1990) and Dunlop & Horrocks (1996) in recognizing a taxon Uropygi containing two orders, Thelyphonida and Schizomida. Rowland & Cooke (1973) split the Thelyphonida into two families, Thelyphonidae and Hypoctonidae, differentiated by carapace keels in the former family which are absent in the latter family. This division is not adopted by all authors. Since the carapace is not preserved in the fossil it is not possible to refer this specimen to either family, both of which have been recorded among the Recent thelyphonid fauna of Brazil (Rowland & Cooke 1973).

Genus *Mesoproctus* new genus

Etymology.—*Meso* from its Mesozoic age and *proctus* from the fossil's overall similarity to the extant genus *Mastigoproctus* which also inhabits arid environments.

Type.—*Mesoproctus rowlandi* new species.

Remarks.—Due to the lack of preserved detail in this specimen it is difficult to diagnose *Mesoproctus* from either Carboniferous or Recent thelyphonids on anything other than its Mesozoic age. The pedipalps are quite robust in *Mesoproctus*, but in isolation this is a poor diagnostic character.

Mesoproctus rowlandi new species
Figs. 1, 2

Etymology.—Named in honor of J. Mark Rowland for his work on whipscorpion systematics and fossil palpigrades and his assistance with this paper.

Type.—Holotype and only specimen. UM No. K28006. From the Lower Cretaceous (Aptian) of the Crato Member of the Santana Formation, Araripe Plateau, Ceará Province, NE Brazil.

Diagnosis.—See remarks above.

Description.—Part only showing specimen in dorso-ventral compression. Length 23.5, prosoma with length 11.0, maximum width 6.8, opisthosoma with maximum length 12.5, maximum width 8.5. Flagellum and posterior end of opisthosoma missing. Carapace morphology, eyes, coxosternal region and opisthosomal segmentation not preserved. Pedipalps and legs generally complete with leg I on both sides folded back and directed posteriorly. All legs preserved laterally with femora II-IV distinctly robust. Pedipalps large and robust. Left pedipalp complete with podomere lengths: trochanter 2.5, femur 4.9, patella 2.6, tibia 4.9 and tarsus 8.5. Right pedipalp lacks tarsus. Left leg I elongate, slender and complete with podomere lengths: femur 6.7, patella 8.9, tibia 9.2, metatarsus 4.0, tarsus 3.0. Tibia and metatarsus ornamented with groove running the length of the podomere. Right leg I with only femur, patella and part of tibia preserved. Left leg II complete with podomere lengths: femur 5.7, patella 2.2, tibia 4.5, metatarsus 1.2, and tarsus 1.3. Right leg II with only femur, patella and part of tibia preserved. Left leg III only preserved as fragment overlying leg I, right leg III complete with podomere lengths: femur 6.0, patella 2.0, tibia 3.8, metatarsus, 1.2 and tarsus 1.5. Leg IV incomplete, only proximal podomeres of left leg IV preserved with podomere lengths: femur 7.0, patella 2.5 and tibia 4.9.

LITERATURE CITED

Brauckmann, C. & L. Koch. 1983. *Prothelyphonus naufragus* n. sp., ein neuer Geißelskorpion aus

dem Namurium (unteres Ober-Karbon) von West-Deutschland. Entomol. Gen., 9:63–73.

Crawford, C.S. & J.L. Cloudsley-Thompson. 1971. Water relations and desiccation-avoiding behaviour in the vinegaroon *Mastigoproctus giganteus* (Arachnida: Uropygi). Entomol. Exp. Appl., 14:99–106.

Dunlop, J.A. & C.A. Horrocks. 1996. A new Upper Carboniferous whip scorpion (Arachnida: Uropygi: Thelyphonida) with a revision of the British Carboniferous Uropygi. Zool. Anz., 234:293–306.

Grimaldi, D.A. & J.G. Maisey. 1990. Introduction. Pp. 195:1–14. *In* Insects from the Santana Formation, Lower Cretaceous, of Brazil. (D.A. Grimaldi, ed.). Bull. American Mus. Nat. Hist.

Maisey, J.G. 1990. Chapter 1. Stratigraphy and depositional environment of the Crato Member (Santana Formation, Lower Cretaceous of N.E. Brazil). Pp. 195:15–19. *In* Insects from the Santana Formation, Lower Cretaceous of Brazil. (D.A. Grimaldi, ed.). Bull. American Mus. Nat. Hist.

Martill, D.M. (ed.). 1993. Fossils of the Santana and Crato Formations, Brazil. Field Guide to Fossils 5. The Palaeontol. Asso., London.

Millot, J. 1949. Ordre des Uropyges. Pp. 533–562. *In* Traité de Zoologie, Anatomie, Systématique, Biologie, Tome VI, Onycophores - Tardigrades - Arthropodes - Trilobitomorphes - Chélicérates. (P.P. Grassé, ed.). Masson et Cie, Paris.

Pocock, R.I. 1894. Notes on the Thelyphonidae contained in the collection of the British Museum. Ann. Mag. Nat. Hist., Series 6, 14:120–134.

Rowland, J.M. & J.A.L. Cooke. 1973. Systematics of the arachnid order Uropygida (=Thelyphonida). J. Arachnol., 1:55–71.

Selden, P.A. 1993. Arthropoda (Aglaspidida, Pycnogonida and Chelicerata). Pp. 297–320. *In* The Fossil Record 2. (M.J. Benton, ed.). Chapman & Hall; London.

Selden, P.A. & W.A. Shear. 1996. The first Mesozoic Solifugae (Arachnida), from the Cretaceous of Brazil, and a redescription of the Palaeozoic solifuge. Palaeontology, 39:583–604.

Shultz, J.W. 1990. Evolutionary morphology and phylogeny of Arachnida. Cladistics, 6:1–38.

LEG AUTOTOMY AND ITS POTENTIAL FITNESS COSTS FOR TWO SPECIES OF HARVESTMEN (ARACHNIDA, OPILIONES)

Cary Guffey[1]:   Department of Biology, PO Box 42451, University of Southwestern Louisiana, Lafayette, Louisiana 70504 USA

ABSTRACT. Leg autotomy often confers immediate benefits on the animal losing its legs, such as escape from a predator, while costs are usually less obvious and accrue long after the leg is lost. I conducted a survey to determine the prevalence and characteristics of leg autotomy in two species of harvestmen, *Leiobunum nigripes* Weed 1892 and *L. vittatum* Say 1821, from May-December 1996 at Chicot State Park, Evangeline Parish, Louisiana. Nearly half of all individuals found were missing at least one leg. There was no significant difference in the median number of legs between months for *L. nigripes*, but differences were found among several months for *L. vittatum*. Either of the second legs was most likely to be lost in both species. These results indicate that leg autotomy is common in harvestmen. Furthermore, these results suggest that the second legs are not as crucial to the survival of harvestmen as previously believed. Leg autotomy may result in a reduction of potential fitness for individuals, but harvestmen may choose to incur these costs rather than risk a catastrophic loss of fitness (e.g., death); that is, leg autotomy may be a bet-hedging strategy for harvestmen.

Autotomy of appendages is widely known for a variety of animal groups, including molluscs (Edmunds 1966), crustaceans (Juanes & Smith 1995), arachnids (e.g., spiders: Formanowicz 1990; harvestmen: Kaestner 1968), insects (Carlberg 1994), echinoderms (e.g., *Thyone briareus* LeSueur 1824: Smith & Greenberg 1973), salamanders (Wake & Dresner 1967), and lizards (Arnold 1984). The effect that autotomy has on the fitness of an individual depends on the sum of the benefits and costs of appendage loss. Benefits may be immediate or nearly so and include distraction of predators (Arnold 1984), escape from a predator's grasp (Arnold 1984), and escape from traps (e.g., spider webs). Costs are spread over a longer period of time and include loss of mobility or balance, reduced ability to escape subsequent encounters with predators, decrease in social status, divergence of energy resources to replacement of the lost appendages, decrease in mating success, and even death in some instances (reviewed in Edmunds 1974; Arnold 1984, 1988; Juanes & Smith 1995).

Harvestmen autotomize their legs but do not regenerate them as either juveniles or adults (Comstock 1920; Kaestner 1968);

therefore, there are no costs associated with regeneration, such as allocation of nutrients to new tissue. However, harvestmen also are not able to recover the benefits that they originally had with the full complement of eight legs. Because harvestmen do not regenerate their legs, when confronted with predators they should be under natural selection to weigh the benefits of leg autotomy against the future costs associated with autotomy, such as subsequent encounters with predators, loss of mobility, loss of foraging ability, or loss of mating opportunities.

The second pair of legs is the longest in *Leiobunum* (Kaestner 1968; Edgar 1990), and these legs are believed to contain the main sensory organs of these animals (Comstock 1920; Edgar 1963; Cloudsley-Thompson 1968). In one study, harvestmen that had lost the second pair of legs were reported to be more reluctant to move, eat, drink, or mate (Sankey & Savory 1974). Cloudsley-Thompson (1968) wrote that the loss of both of the second pair of legs quickly results in death. Given the reported importance of the second pair of legs, I predict that harvestmen should be particularly reluctant to autotomize this pair compared to the other pairs.

In general, three different life histories can be found in Opiliones (Todd 1949). (1) Eggs laid the previous autumn hatch in the spring.

[1] Current address: Our Lady of the Lake University, 411 SW 24th St., San Antonio, Texas 78207 USA.

The animals mature over the summer and lay eggs in the autumn, then adults may or may not die at the first frost (e.g., *Leiobunum nigripes* Weed 1892). This results in an overlap of generations in some species (e.g., *Phalangium opilio* Linnaeus 1758: Clingenpeel & Edgar 1966). (2) Eggs hatch in the autumn and the young overwinter. The young mature during the following summer, lay their eggs, then die before the clutches hatch. Clingenpeel & Edgar (1966) used populations of *Leiobunum politum* Weed 1889 and *L. vittatum* Say 1821 from Michigan as examples, but the latter species appears to follow pattern 1 in south central Louisiana (pers. obs.). (3) As in the previous case, the eggs hatch in the autumn and the young overwinter. Eggs are laid the following autumn, but the adults do not die until after the eggs hatch, resulting in an overlap of generations (e.g., *L. townsendi* Weed 1893: Cokendolpher et al. 1993). Harvestmen are ametabolous, and the young undergo 5–8 molts before reaching adulthood (Edgar 1971; Kaestner 1968) with the first molt taking place within hours of hatching (Edgar 1971).

Both *L. vittatum* and *L. nigripes* were collected throughout the year at Chicot State Park, Evangeline Parish, Louisiana; but it was common to find only adult *L. vittatum* from late November to early January and to find only juvenile *L. nigripes* from early January to mid-February. *Leiobunum nigripes* emerged 1–2 months earlier than *L. vittatum*.

In this study, I conducted field observations of *L. nigripes* and *L. vittatum* to determine the prevalence of leg autotomy in these species, which legs are most likely to be autotomized, and what costs might be associated with leg autotomy. I predicted that: (1) the proportion of individuals missing legs should increase with age, (2) the second legs should be the least likely to be autotomized, and (3) individuals found mating should be more likely to have all eight legs than those individuals found alone.

METHODS

Study animals.—I observed juveniles and adults of *L. nigripes* and *L. vittatum* at Chicot State Park, Evangeline Parish, Louisiana between May and December 1996. Individuals were collected from cabins, vegetation, and 10.2 × 10.2 × 50.0 cm wooden posts. I re-

corded location, number of legs, which legs were missing, and whether or not collected individuals were found in the copulatory position. Both species in this study are sexually dimorphic, but the characters used to identify the sexes of *L. nigripes* (size, color; pers. obs.) are not as reliable as that used for *L. vittatum* (size of pedipalps; Davis 1935). Any animals for which the sex was uncertain were removed from comparisons based on sex. I released all animals near the sites at which they were collected. A previous mark-recapture study indicated that <10% of marked animals were caught at the site at which they were marked after 24 h and <1% were recaptured after two weeks (unpubl. data); therefore, pseudoreplication due to resampling should have been negligible.

Comparisons between months.—I used a Kruskal-Wallis one-way ANOVA by rank (Siegel & Castellan 1988) to determine if there was any significant difference for each species in the number of legs present among months. When a significant difference was detected, I used a multiple comparisons test (Siegel & Castellan 1988) to locate significant differences between months. These tests were two-tailed and the test statistics were adjusted for ties with $\alpha = 0.05$.

Comparisons of leg pairs.—I summed the number of times that either leg of a particular pair was autotomized and compared these observed values to an expected value obtained by assuming that each pair was equally likely to lose a member. The probability (P) that either leg of any particular pair would be lost was 0.25. This value was calculated as follows

$$P(X_L \text{ or } X_R) = P(X_L) + P(X_R) = \frac{1}{8} + \frac{1}{8} = \frac{2}{8} = 0.25$$

where X is any particular leg pair, L indicates left, and R indicates right. This null hypothesis was evaluated for both species with a Chi-square goodness of fit test (Freund & Simon 1992) and compared to $\alpha = 0.05$.

I compared the number of individuals missing both legs of the second pair to an expected probability of 0.036 (again assuming an equal likelihood that any leg would be autotomized). This probability was calculated as follows

$$P(X) = P(X_1) \text{ and } P(X_2) = P(X_1)P(X_2) = (\frac{2}{8})(\frac{1}{7}) = 0.036$$

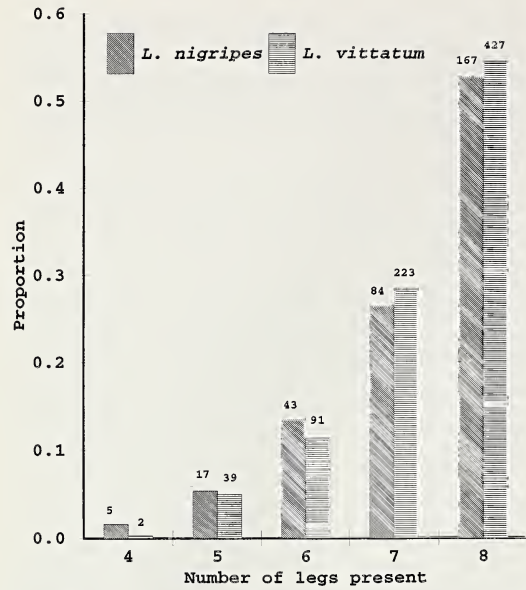where X is any particular leg pair. I used a

Figure 1.—The incidence of leg autotomy in two species of harvestmen from Evangeline Parish, Louisiana, May-December 1996. The proportion of individuals with a given number of legs was not significantly different between the two species. The numbers above the bars indicate sample sizes.

Figure 2.—A comparison of leg number by species and sex. There was no significant difference in proportions between the sexes for either *Leiobunum nigripes* or *Leiobunum vittatum*. The dashed vertical line separates the data for males from that for females in each graph. The numbers above the bars indicate sample sizes.

one-tailed binomial test (Siegel & Castellan 1988) to evaluate the null hypothesis that the observed values for the loss of the second pair of legs came from a binomial distribution with $P = 0.036$. I compared the test results to $\alpha = 0.05$.

Comparisons of mating pairs with lone individuals.—I counted the number of legs of those individuals of *L. vittatum* found in the copulatory position and those found alone on 24 and 31 October 1996. Copulation in both *L. nigripes* and *L. vittatum* occurs when the male grasps the female's prosoma with his pedipalps and repeatedly attempts to insert his penis under the genital operculum of the female (*L. nigripes*: pers. obs.; *L. vittatum*: Edgar 1971; Macías-Ordóñez 1997). I compared the number of legs of those animals found alone to those found in the copulatory position; but because of the small sample sizes of those animals with seven or fewer legs, I pooled all of those animals and compared them to animals with eight legs in my statistical analyses. I tested the null hypothesis of no significant difference with a *G*-test of independence with the Williams correction (So-

kal & Rohlf 1995). The test statistic was compared to $\alpha = 0.05$.

RESULTS

Nearly half of all harvestmen found were missing at least one leg (Fig. 1). There was no significant difference between *L. nigripes* and *L. vittatum* in the proportion of individuals at each level of leg loss ($\chi^2 = 5.65$, $P = 0.226$). Likewise, there was no significant difference between the sexes in the proportion of individuals missing a particular number of legs within either *L. nigripes* (Fig. 2A; $\chi^2 = 0.53$, $P = 0.768$) or *L. vittatum* (Fig. 2B; $\chi^2 = 1.77$, $P = 0.621$). The ratio of males to females was 1.3:1 ($n = 136$) for *L. nigripes* and 1.4:1 ($n = 897$) for *L. vittatum*.

There was no significant difference in the median number of legs among months for *L. nigripes* (Table 1; $df = 7$, $KW = 10.07$). A significant difference was detected among months in the median number of legs for *L. vittatum* (Table 2; $df = 7$, $KW = 43.01$). A multiple comparisons test indicated that those

Table 1.—Leg number for *Leiobunum nigripes* by month. A Kruskal-Wallis one-way ANOVA by rank, adjusted for ties, yielded $P = 0.186$.

Month	n	Mean (± SE)	Median
May	109	7.1 (0.10)	7.0
June	42	7.0 (0.16)	7.0
July	46	7.4 (0.12)	8.0
August	39	7.4 (0.15)	8.0
September	31	7.5 (0.17)	8.0
October	24	7.2 (0.23)	8.0
November	21	7.4 (0.19)	8.0
December	4	7.8 (0.25)	8.0

Table 2.—Leg number for *Leiobunum vittatum* by month. A Kruskal-Wallis one-way ANOVA by rank, adjusted for ties, yielded $P < 0.001$. Like superscripts indicate no significant difference in medians between those months as detected by a multiple comparisons test.

Month	n	Mean (± SE)	Median
May	100	7.6 (0.07)	8.0[A]
June	31	7.4 (0.14)	8.0[AB]
July	119	7.5 (0.07)	8.0[A]
August	45	7.4 (0.10)	8.0[AB]
September	173	7.4 (0.06)	8.0[A]
October	58	7.2 (0.14)	8.0[AB]
November	102	7.2 (0.09)	7.5[AB]
December	156	6.9 (0.08)	7.0[B]

animals found in December had significantly fewer legs than those in May, July, and September (Table 2).

For both *L. nigripes* and *L. vittatum,* I determined that legs were not equally likely to be lost (Fig. 3; *L. nigripes*: $\chi^2 = 19.93$, $P < 0.001$; *L. vittatum*: $\chi^2 = 42.06$, $P < 0.001$). A leg was most likely to be missing from the second pair in both species (Fig. 3). The second pair of legs was missing significantly more often than expected for both *L. nigripes* ($n = 26$, $k = 6$, $P < 0.001$) and *L. vittatum* ($n = 86$, $k = 6$, $P = 0.034$).

I found no significant difference in leg number for those males of *L. vittatum* found in a copulatory posture ($n = 21$) compared to those found alone (Fig. 4A; $G = 0.015$, $P = 0.902$). Likewise, there was no significant difference in leg number for those females found in the copulatory position ($n = 20$) and those found alone (Fig. 4B; $\chi^2 = 3.10$, $P = 0.078$). There was no significant difference between the sexes of *L. vittatum* in the numbers of animals with eight legs found alone ($G = 3.006$, $P = 0.083$).

DISCUSSION

Because *Leiobunum* is typically univoltine (Clingenpeel & Edgar 1966; Cokendolpher et al. 1993) and does not regenerate autotomized legs, I predicted that the average number of legs per individual would decrease with time. Contrary to expectations, the median number of legs did not decrease in *L. nigripes* over the course of the study period. However, *Leiobunum vittatum* found in December had significantly fewer legs than those found in May, July, and September.

The second pair of legs plays an important

role in sensing the surrounding environment of individuals of *Leiobunum* (Comstock 1920; Sankey & Savory 1974). Therefore, I predicted that harvestmen are under pressure from natural selection to protect those legs. However, the results presented here indicate that when only one leg is autotomized, the lost limb is most likely to be from the second pair
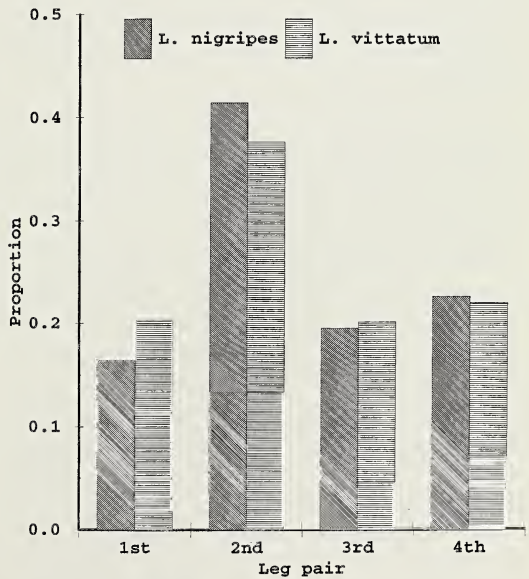

Figure 3.—The proportion of each pair of legs represented in the sample of those harvestmen missing at least one leg. The observed numbers were significantly different from the values expected given an equal chance of autotomy for all legs. The expected proportion is represented by a solid horizontal line across the middle of the graph. The numbers above the bars indicate sample sizes.

Males

8 legs   < 8 legs

mating   alone

Females
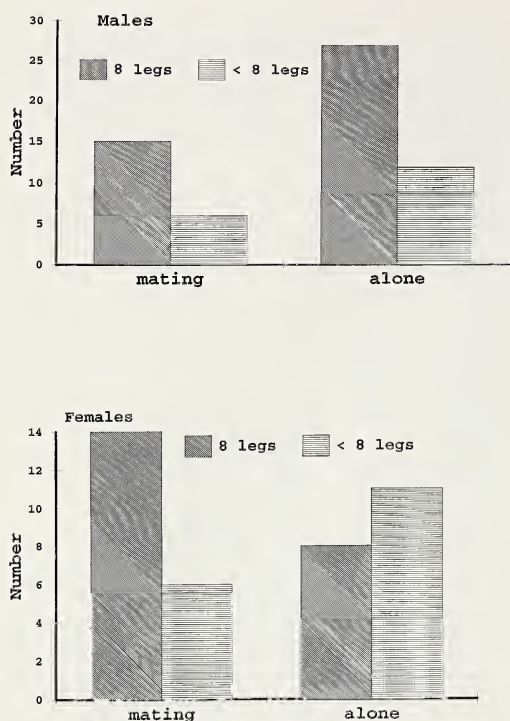
8 legs   < 8 legs

mating   alone

Figure 4.—A comparison of leg numbers of those individuals of *Leiobunum vittatum* found either mating or alone on 24 and 31 October 1996. There was no significant difference in the number of animals found either mating or alone for males or females.

of legs. Also, the second pair of legs is significantly more likely to be lost than expected if one assumes that all legs have an equal probability of being lost.

My final prediction was that significantly more individuals of *L. vittatum* found mating would have all eight legs than those individuals found alone. This would be expected if legs are important for finding mates or in intrasexual contests. I found no significant difference in the proportions of individuals with eight legs found mating compared to those found alone for either sex.

Leg autotomy is common in *L. nigripes* and *L. vittatum*. Leg loss may be caused by (1) intraspecific or intrasexual battles, (2) poor nutrition resulting in loss of legs during molting, or (3) different types of predation pressures such as direct attack or loss in webs. Males of *L. vittatum* fight over access to oviposition sites by shoving one another with their bodies, only rarely grasping one another by the legs (Macías-Ordóñez 1997). There-

fore, intraspecific or intrasexual combat do not appear to be significant causes of leg autotomy.

If nutrition is responsible for a significant degree of leg loss, then the average number of legs present per animal should decrease during juvenile stages (January-July) but should not change significantly after the final molt (*ca.* July). My data do not cover the earliest molts, but I found no significant differences in leg number between the later instars and adults, suggesting that nutritional state is not the primary cause of loss of legs in older juveniles.

If the risk of predation is equal between species and between sexes within species, then this would explain why there is no significant difference in leg number between these groups. Furthermore, because the second legs are longer than any others in *Leiobunum* (Kaestner 1968; Edgar 1990) and these legs are the first part of the harvestman to move when individuals are disturbed (Comstock 1920; Sankey & Savory 1974), these legs are most likely to come into contact with predators or traps and thus to be autotomized. Spivak & Politis (1989) found that the longest and most exposed limbs of crabs were the most likely limbs to be autotomized. If the second legs are the most important sensory organs of harvestmen, then autotomy may result in a substantial cost to these animals in terms of loss of sensory ability.

Though the data presented here indicate that there was no significant difference in leg number between *L. vittatum* found mating and those found alone, I did not have enough individuals missing two or more legs to make comparisons at specific levels of leg autotomy (e.g., eight legs *vs.* six legs). There may be a cost in fitness due to reduced mating success as a result of leg autotomy, especially when two or more legs are missing. Such costs may be caused by a reduced ability (1) to find mates because of lessened mobility or diminished sensory capacity, (2) to find oviposition or mating sites, or (3) to prevail during intrasexual encounters. Mates and oviposition sites are apparently identified only through direct contact with the legs (Macías-Ordóñez 1997). Therefore, leg autotomy has the potential to impose a significant cost on the future fitness of both males and females of *L. vittatum*.

Males of *L. vittatum* with more legs than their opponents win significantly more male-male contests when both males have equal territorial status, but the contest winners do not achieve increased mating success (Macías-Ordóñez 1997). Macías-Ordóñez (1997) conducted his research at a site in which oviposition (and hence, mating) sites were not limited. Therefore, contest losers were soon able to find other mating sites. The outcome of contests, and thereby leg number, might be more important in those areas in which oviposition sites and access to females are limited or when male-male contests involve individuals with unequal territorial status. I could not determine if the oviposition sites for the populations in this study are limited.

Bet-hedging strategies are those behaviors that decrease the expected fitness of an individual but with the benefit of reducing the risk of a total loss of fitness; that is, lower potential fitness is offset by a reduction in the variance of fitness (Seger & Brockmann 1987). Leg autotomy may reduce an individual's expected fitness by decreasing its sensory capabilities (unpubl. data). It is also possible that individual fitness may decrease as a result of autotomy due to reduced mobility or increased risk of capture during subsequent encounters with predators. Harvestmen that autotomize their legs presumably benefit by avoiding being eaten by spiders or other predators. The interaction between the immediate benefits obtained from leg autotomy and its later costs fits the model for a bet-hedging strategy (Seger & Brockmann 1987).

To this point, I have considered only the hypothesis that leg autotomy imposes a cost on those harvestmen that lose legs. An alternative hypothesis is that harvestmen have enough legs such that loss of one or a few of them does not cause any substantial reduction in the expected fitness of an individual—in other words, harvestmen may have spare legs. Most of the data presented above show only the potential for a reduction in fitness. Within each sex, there was no significant difference in the proportions of individuals found alone or mating. The spare-leg hypothesis would lead to the prediction that when animals are divided into groups with either all eight legs present or those missing one or a few legs, as reported in this study, there would be no significant differences detectable. Instead, differ-

ences would only be detectable after a certain number of legs are lost, requiring a finer resolution of the categories compared.

It remains to be determined (1) if leg autotomy at any level is costly to harvestmen and, if it is costly, (2) at what point leg loss becomes so costly that a harvestman would be just as well off risking a catastrophic failure of reproduction (e.g., because of death by predation). While the present study does not quantify the costs associated with leg autotomy, it suggests that such costs exist and leads to an expectation that there is some level of leg autotomy at which harvestmen obtain a greater payoff for not losing any additional legs.

ACKNOWLEDGMENTS

LITERATURE CITED

Arnold, E.N. 1984. Evolutionary aspects of tail shedding in lizards and their relatives. J. Nat. Hist., 18:127–169.

Arnold, E.N. 1988. Caudal autotomy as a defense. Pp. 235–273, *In* Biology of the Reptilia, Vol. 16, Ecology B (C. Gans & R. B. Huey, eds.). A.R. Liss, New York.

Carlberg, U. 1994. Cost of autotomy in the Phasmida (Insecta). II. Species with high autotomy frequency. Zool. Anz., 232:41–49.

Clingenpeel, L.W. & A.L. Edgar. 1966. Certain ecological aspects of *Phalangium opilio* (Arthropoda: Opiliones). Pap. Michigan Acad. Sci. Arts Lett., 51:119–126.

Cloudsley-Thompson, J.L. 1968. Spiders, Scorpi-

ons, Centipedes and Mites. Pergamon Press, Oxford, United Kingdom.

Cokendolpher, J.C., W.P. MacKay & M.H. Muma. 1993. Seasonal population phenology and habitat preferences of montane harvestmen (Arachnida: Opiliones) from southwestern New Mexico. Southwest. Nat., 38:236–240.

Comstock, J.H. 1920. The Spider Book. Doubleday, Page & Co., Garden City, New York.

Davis, N.W. 1935. A revision of the genus *Leiobunum* (Opiliones) of the United States. American Midl. Nat., 15:662–705.

Edgar, A.L. 1963. Proprioception in the legs of phalangids. Biol. Bull., 124:262–267.

Edgar, A.L. 1971. Studies on the biology and ecology of Michigan Phalangida (Opiliones). Misc. Publ. Mus. Zoo. Univ. Michigan, 144:1–64.

Edgar, A.L. 1990. Opiliones (Phalangida). Pp. 529–581, *In* Soil Biology Guide (D.L. Dindal, ed.). John Wiley & Sons, New York.

Edmunds, M. 1966. Protective mechanisms in the Eolidacea (Mollusca Nudibranchia). J. Linn. Soc. (Zool.), 46:27–71.

Edmunds, M. 1974. Defence in Animals. Longman Group Limited, New York.

Formanowicz Jr., D.R. 1990. The antipredator efficacy of spider leg autotomy. Anim. Behav., 40: 400–401.

Freund, J.E. & G.A. Simon. 1992. Modern Elementary Statistics, 8th ed. Prentice Hall, Englewood Cliffs, New Jersey.

Juanes, F. & L.D. Smith. 1995. The ecological consequences of limb damage and loss in decapod crustaceans: a review and prospectus. J. Exp. Mar. Biol. Ecol., 193:197–223.

Kaestner, A. 1968. Invertebrate Zoology, Vol. II: Arthropod Relatives, Chelicerata, Myriapoda (translated by H.W. Levi & L.R. Levi). Interscience Publishers, New York.

Macías-Ordóñez, R. 1997. The mating system of *Leiobunum vittatum* Say 1821 (Arachnida: Opiliones: Palpatores): resource defense polygyny in the striped harvestman. Ph.D. Dissertation, Lehigh University, Bethlehem, Pennsylvania.

Sankey, J.H.P. & T.H. Savory. 1974. British Harvestmen. Academic Press, New York.

Seger, J. & H.J. Brockmann. 1987. What is bet-hedging? Oxford Surv. Evol. Biol., 4:182–211.

Siegel, S. & N.J. Castellan, Jr. 1988. Nonparametric Statistics for the Behavioral Sciences, 2nd ed. McGraw-Hill, Inc., New York.

Sokal, R.R. & F.J. Rohlf. 1995. Biometry, 3d ed. W.H. Freeman & Co., New York.

Smith, Jr., G.N. & M.J. Greenberg. 1973. Chemical control of the evisceration process in *Thyone briareus*. Biol. Bull., 144:421–436.

Spivak, E.D. & M.A. Politis. 1989. High incidence of limb autotomy in a crab population from a coastal lagoon in the province of Buenos Aires, Argentina. Canadian J. Zool., 67:1976–1985.

Todd, V. 1949. The habits and ecology of the British harvestmen (Arachnida, Opiliones), with special reference to those of the Oxford district. J. Anim. Ecol., 18:209–229.

Wake, D.B. & I.G. Dresner. 1967. Functional morphology and evolution of tail autotomy in salamanders. J. Morphol., 122:265–306.

GROUND SURFACE SPIDER FAUNA IN
FLORIDA SANDHILL COMMUNITIES

David T. Corey: Science Department, Midlands Technical College, P.O. Box 2408, Columbia, South Carolina 29202 USA

I. Jack Stout: Department of Biology, University of Central Florida, Orlando, Florida 32816-2368 USA

G.B. Edwards: Florida State Collection of Arthropods, Division of Plant Industry, Florida Department of Agriculture & Consumer Services, P.O. Box 147100, 1911 SW 34th St., Gainesville, Florida 32614-7100 USA

ABSTRACT. Spiders were collected from the forest floor surface using pitfall traps (cans and buckets) and funnel traps at 12 study sites selected to represent the sandhill community of north and central Florida. A total of 5236 spiders was collected, which included 23 families, 92 genera, and 154 species. The largest number of individuals (528) was collected at Orange City and the largest number of species (48) was collected at the most northern site, Suwannee River State Park. Species richness, abundance, similarity and seasonal variation were compared among the study sites. Lycosidae comprised 75.2% of the total number of spiders collected. Four species were collected at all 12 sites: the lycosids *Lycosa ammophila*, *Schizocosa duplex*, and *S. segregata*, and the salticid *Habrocestum xerophilum*. Eighty-three (53.9%) of the 154 species were collected at only one site.

In the past, sandhills of the southeastern coastal plain of North America supported an ecosystem type variously referenced as "high pine land" (Harper 1927), "sandhill country" (Wells & Shunk 1931), or "longleaf pine-turkey oak sandhills" (Laessle 1942). Laessle (1958), Myers (1985, 1990) and Stout & Marion (1993) provided a general summary of this xeric upland community type (Fig. 1). The tree layer is dominated by longleaf pine, *Pinus palustris* Mill. and turkey oak, *Quercus laevis* Walt. The understory consists chiefly of wiregrass, *Aristida stricta* Michx. and a rich assemblage of other grasses and herbs (Platt et al. 1988).

Examples of this abstract community type are found from eastern Virginia to extreme eastern Texas and peninsular Florida (Stout and Marion 1993). Development and fragmentation of the community began over 200 years ago and continues to this day as remnant stands are converted to housing developments and shopping malls. Approximately 20% of the historic landscape of Florida was occupied by the sandhill community, but nearly 90% of this community has been lost in the last 50 years (Cox et al. 1994). The loss of biodiver-sity associated with landscape development has been documented by Burgess & Sharpe (1981), Wilcove et al. (1986), Whitcomb (1987) and Saunders et al. (1991).

In order to study the loss of biodiversity in the Florida sandhill communities, we thought it necessary to obtain knowledge of the existing fauna. We were able to sample 12 different sites in peninsular Florida, using a variety of sampling techniques in order to maximize the number of species of ground fauna collected. One of the major groups of organisms collected was the spiders.

The biodiversity of arachnids associated with the forest floor of xeric pineland communities of Florida is poorly known. Corey & Stout (1990, 1992) reported on the scorpion, pseudoscorpion, opilionid, uropygid, solpugid, mite, tick, centipede and millipede faunas in sandhill communities. Corey & Taylor (1987, 1988, 1989) reported on the scorpion, pseudoscorpion, opilionid and spider faunas in pond pine, sand pine scrub and pine flatwoods communities of Florida. Lowrie reported on spiders from the Pensacola area of Florida (1963, 1971). Muma (1973, 1975) sampled the ground surface spider fauna in four central

Figure 1.—Typical sandhill community vegetation (late winter, Levy County, Florida).

Florida communities (pine flatwoods, sand pine dune, citrus groves, residential). Rey & McCoy (1983) studied the spiders and pseudoscorpions in northwest Florida salt marshes. The purpose of this paper is to document the species composition, diversity, guild composition and seasonal abundance of spiders associated with the forest floor of longleaf pine-turkey oak sandhill communities of peninsular Florida. Our approach is similar to that of Barnes & Barnes (1955) in that we are considering an abstract community type with a wide geographic range. In another paper, we will discuss the effects of area and isolation on species richness of forest floor arthropods in these xeric pinelands.

METHODS

Study sites.—The ground fauna of twelve sandhill sites was sampled between November 1986 and December 1988 (Fig. 2). Study site selection was subjective and depended on several attributes: 1) internal consistency of vegetative cover (tree, shrub and ground layer), 2) nature of the surrounding habitat, 3) area, 4) security from disturbance, and 5) accessibility. Each study site was sampled for four

days during each of four periods: September-November (= autumn), December-February (= winter), March-May (= spring) and June-August (= summer).

Sampling locations included: San Felasco Hammock (SF) and Morningside Nature Center (MS), Alachua County; Spruce Creek Preserve (SC) and Orange City (OC), Volusia County; Bok Tower Gardens (BT), Polk County; O'leno State Park (OL), Columbia County; Suwannee River State Park (SR), Suwannee County; Wekiwa Springs State Park (WS), Orange County; Sandhill Boy Scout Reservation (BS) and Janet Butterfield Brooks Preserve (JB), Hernando County; Interlachen (IL), Putnam County; Starkey Well Field Area (SW), Pasco County.

Sampling.—Spiders were collected using three different techniques. Five pitfall traps with a diameter of 15.5 cm (3.79-liter tin can) were randomly placed (Post & Riechert 1977) in each study site during the first collecting period. During subsequent collections the traps were placed in the same location as in the first collecting period. Cans were buried flush with the soil surface and partly filled
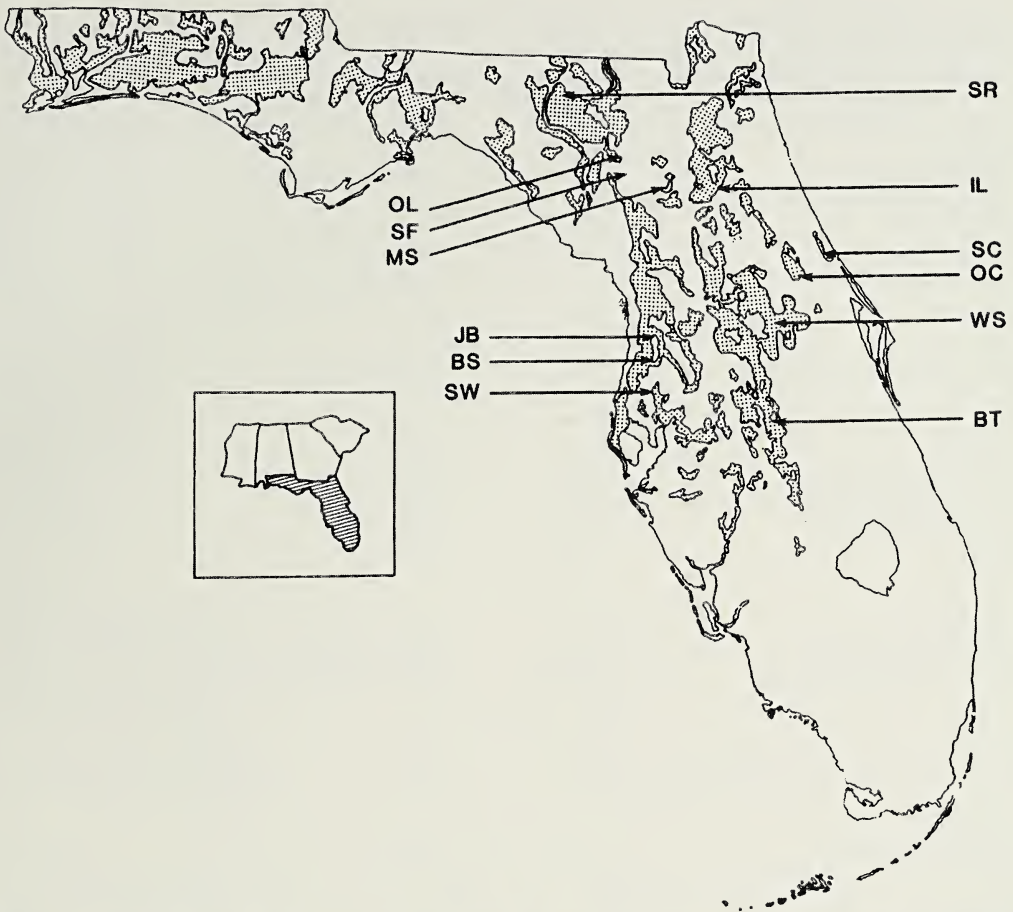
Figure 2.—Sandhill study site locations in Florida. Sampling locations are: Suwannee River State Park (SR), O'leno State Park (OL), San Felasco Hammock (SF), Morningside Nature Center (MS), Interlachen (IL), Spruce Creek Preserve (SC), Orange City (OC), Wekiwa Springs State Park (WS), Janet Butterfield Brooks Preserve (JB), Sandhill Boy Scout Reservation (BS), Starkey Well Field Area (SW), Bok Tower Gardens (BT). Sandhill distributions (stippled) are based on Davis (1980) and do not reflect minor sites of this community due to the scale of the illustration.

with 0.47 liter of a mixture of 2 parts ethylene glycol, 1 part water and 1 part 95% ethanol. A slightly elevated wooden cover protected each trap from disturbance. A similar but more complex technique designed to capture herpetofauna ("herp arrays") consisted of 16 buckets and 16 funnel traps associated with drift fences (Campbell & Christman 1982). Each of two arrays per site consisted of four sheet metal arms (7.6 m long) oriented in the cardinal directions. A pitfall trap with a diameter of 29.0 cm (21.4 liter plastic bucket) was buried flush with the surface at the end of each arm (2 per arm). No preservative was added to the buckets. Funnel traps (10 × 100 cm) made of fine-mesh wire window screen-

ing were placed on the ground on each side of a drift fence arm at the midpoint. Spiders were removed from the buckets and funnel traps daily and preserved in ethanol. A total of 95 samples was taken; SW was sampled on seven rather than eight occasions.

Identification.—Adult spiders were identified to the lowest possible taxon. Most immatures were identified to family only. Voucher specimens have been deposited in the Florida State Collection of Arthropods.

Habitat analysis.—Tree, shrub, and herbaceous vegetation was sampled to determine if the abundance of spiders was correlated with these habitat features. Internal site homogeneity allowed us to use a completely ran-

Table 1.—Spider abundance collected in Florida sandhills using pitfall traps (P), buckets (B), and funnel traps (F). See text for study site abbreviations.

Species	Method	Collection Sites	Totals
Ctenizidae			2
Myrmeciophila sp.	P, B	MS, BT, OL, SW	13
Ummidia audouini (Lucas)	B	WS	1
Ummidia sp. #1	B	SF, OL, JB	9
Ummidia sp. #2	B	SF, OL	4
Ummidia sp. #3	B	OC, SC, WS, OL, IN, JB	21
Totals			50
Uloboridae			2
Uloborus glomosus (Walck.)	P, B	MS, JB, SW	4
Totals			6
Dictynidae			1
Dictyna formidolosa G&I	B	OC	1
Lathys immaculata C&I	B	OL	1
Lathys albida Gertsch	P	SC	1
Lathys sp.	B	SC	1
Totals			5
Amaurobiidae			4
Metaltella simoni (Keys.)	B	MS, SR, BT	20
Titanoeca brunnea Emerton	P, B	OC, MS, SR, IN, SW	7
Totals			31
Oonopidae			
Heteroonops spinimanus (Simon)	B	SF	1
Totals			1
Deinopidae			
Deinopis spinosa Marx	B	MS	1
Totals			1
Theridiidae			20
Achaearanea porteri (Banks)	P, B, F	SC, MS, WS, OL, IN, JB, BS	26
Coleosoma acutiventer (Keys.)	B	MS	1
Crustulina altera G&A	B	OC	2
Dipoena abdita G&M	P	SR	1
D. nigra (Emerton)	P	SR, BS	2
Euryopis funebris (Hentz)	P	SR	1
Lactrodectus mactans (Fabr.)	P, B	SC, MS, IN, JB, BS, SW	14
L. geometricus CL Koch	B	SR, BT, BS	5
Pholcomma hirsutum Emerton	P	SC	1
Steatoda quadrimaculata (OPC)	B	SR	1
Stemmops bicolor OPC	P	WS, OL	2
Theridion cinctipes Banks	P	SR	1
Tidarren sisyphoides (Walck.)	B	SF	1
Totals			78
Linyphiidae			58
Centromerus tennapax (Barrows)	P, B	OC, OL	2
Ceratinops crenata Emerton	P	BS	1
Ceratinopsis sp.	P	SW	1
Eperigone maculata (Banks)	P	OC, SC, MS, SR, JB, SW	15
Erigone autumnalis Emerton	P	JB	1
Frontinella pyramitela (Walck.)	B	JB	1
Grammonota texana (Banks)	B	OL	1
Tapinocyba hortensis (Emerton)	P	MS, SW	2
Tennesseellum formicum (Emerton)	P	OL	1
Meioneta unimaculata (Banks)	P	OC, SF, MS, SR, OL, JB	9

Table 1.—Continued.

Species	Method	Collection Sites	Totals
Meioneta sp. #1	P	OC	1
Meioneta sp. #2	P, B	SF, MS, IN	3
Meioneta sp. #3	P	SF	2
Meioneta sp. #4	P	SC	1
Meioneta sp. #5	P	BS	1
Meioneta sp. #6	P	BS	1
Species #1	P	JB	1
Species #2	P	IN	1
Species #3	P	SR	2
Species #4	B	JB	2
Species #5	B	SC	1
Species #6	P	SC	1
Species #7	P	MS	1
Species #8	P	WS	1
Species #9	B	OL	1
Species #10	P	OL	2
Totals			114
Araneidae			9
Acacesia hamata (Hentz)	P	MS	1
Acanthepeira stellata (Marx)	P, F	OL, JB	2
Argiope aurantia Lucas	B	WS	1
Eustala anastera (Walck.)	P	SR	1
Hypsosinga rubens (Hentz)	B	OC	1
Micrathena gracilis (Marx)	B	OL	1
Wagneriana tauricornis (OPC)	P	WS, OL	2
Totals			18
Agelenidae			1
Agelenopsis barrowsi (Gertsch)	B, F	SF, MS, IN, JB, BS	23
Circurina varians G&M	P, B	OC	5
Totals			29
Hahniidae			1
Hahnia cinerea Emerton	P, B	OC, SR, JB, BS	13
Neoantistea agilis (Keys.)	P, B	SR, OL	3
Totals			17
Mimetidae			
Ero pensacolae Ivie & Barrows	B	SR	1
Totals			1
Lycosidae			1148
Arctosa incerta Bryant	P, B	OC, WS, SR, OL	16
A. littoralis (Hentz)	P, B	SF, MS, WS, BT, OL, JB, SW	81
Geolycosa fatifera (Hentz)	B	IN	1
G. patellonigra Wallace	B	SF, WS	2
G. xera McCrone	B	OC, MS, BT, JB, SW	21
Gladicosa pulchra (Keys.)	P, B, F	OC, SC, SF, MS, WS, BT, OL, IN, BS	37
Lycosa ammophila Wallace	P, B, F	OS, SC, SF, MS, WS, SR, BT, OL, IN, JB, BS, SW	1555
L. carolinensis Walck.	P, B	OC, SC, MS, SR, OL, IN, JB, BS, SW	106
L. lenta Hentz	B	SW	1
L. osceola G&W	B	SC, SF, BS	20
Pardosa milvina (Hentz)	B, F	SF, SR, IN	13
P. parvula Banks	P	SR	2
Pirata spiniger (Simon)	P, B	MS, SR, OL, JB	9

Table 1.—Continued.

Species	Method	Collection Sites	Totals
Rabidosa punctulata (Hentz)	B, F	SC, BT, IN, BS, SW	24
R. rabida (Walck.)	B	SC, SR, BT, JB, BS	12
Schizocosa duplex Chamberlin	P, B, F	OC, SC, SF, MS, WS, SR, BT, OL, IN, JB, BS, SW	711
S. avida (Walck.)	P, B, F	OC, MS, BT, SW	11
S. segregata G&W	P, B, F	OC, SC, SF, MS, WS, SR, BT, OL, IN, JB, BS, SW	74
Sosippus floridanus Simon	P, B, F	OC, SF, MS, WS, BT, OL, JB, BS, SW	93
S. mimus Chamberlin	F	SR	1
Trochosa parthenus (Chamberlin)	P	SR	1
Totals			3939
Oxyopidae			22
Hamataliwa grisea Keys.	B	OC	1
Oxyopes acleistus Chamberlin	B	BT, OL, SW	3
Peucetia viridans (Hentz)	B	BT	1
Totals			26
Gnaphosidae			54
Callilepis imbecilla (Keys.)	P, B	OC, SC, MS, WS, SR, BT, OL, IN	24
Cesonia bilineata (Hentz)	P	BT	5
Drassyllus aprilinus (Banks)	P, B, F	SC, SF, MS, WS, BT, IN, BS, SW	44
D. seminolus C&G	P	SF	1
D. alachua P&S	P	SF	1
D. eremitus Chamberlin	P	SR	1
D. lepidus (Banks)	B	MS	3
Gnaphosa sericata (L. Koch)	P, B	OC, SR, BT	3
Herpyllus emertoni Bryant	P	SC	1
Haplodrassus signifer (CL Koch)	P, B	OC, SC, SF, WS, SR, BT, IN, BS	37
Litopyllus temporarius Chamberlin	P	SF	1
Micaria punctata Banks	P	MS	1
M. seminola Gertsch	P	OC	2
Sergiolus capulatus (Walck.)	B	WS	1
S. cyaneiventris Simon	P	SW	1
Talanites exilineae (P&S)	P, B	OC, SF, MS, WS, SR, BT, OL, IN, BS, SW	37
Zelotes hentzi Barrows	B	BT	10
Z. pseustes Chamberlin	P, B	OC, SC, SF, SR, IN, JB, BS	54
Z. lymnophilus Chamberlin	P, B	OC, SFMS, WS, BT, OL, IN, SW	42
Z. ocala P&S	P	OC, IN	4
Z. florodes P&S	P	BT	1
Totals			328
Clubionidae			21
Castianeira amoena (CL Koch)	P	SR	2
C. descripta (Hentz)	P, B	OC, SC, SF, MS, WS, SR, BT, IN, JB, BS, SW	39
C. longipalpus (Hentz)	P, B	MS, SR, IN	4
C. cingulata (CL Koch)	B	OC, SC, JB, BS	5
C. crocata (Hentz)	B	OL, SW	2
C. floridana (Banks)	P	MS, SR, OL, JB, SW	8
C. gertschi Kaston	P	WS	1

Table 1.—Continued.

Species	Method	Collection Sites	Totals
Clubiona pikei Gertsch	B	SR, OL	2
Elaver excepta (L. Koch)	P, F	OC, OL	2
Myrmecotypus lineatus (Emerton)	B	SR, IN	2
Phrurotimpus alarius (Hentz)	P	SC, MS, SW	7
P. minutus (Banks)	P, B	OC, SF, MS, OL	28
P. borealis (Emerton)	P, B	SC, SR, IN, JB, BS	9
Scotinella sp. #1	B	OC	1
Scotinella sp. #2	P	WS	1
Strotarchus piscatoria (Hentz)	B	MS	1
Totals			135
Pisauridae			1
Dolomedes okefinokensis Bishop	B, F	SC, IN, SW	3
D. albineus Hentz	B	SR	1
Pisaurina mira (Walck.)	B, F	OC, BS	5
P. undulata (Keys.)	F	BT	1
Totals			11
Anyphaenidae			1
Hibana velox (Becker)	P, B	MS, BT, BS	5
Totals			6
Ctenidae			
Ctenus captiosus Gertsch	P	OC	2
Totals			2
Heteropodidae			
Tentabunda cubana (Banks)	P, B, F	OC, SC, SF, BT, OL, BS	12
Totals			12
Thomisidae			5
Ozyptila floridana Banks	P, B	SC, MS, SR, BT, BS	47
Xysticus sp.	B, F	SC, MS, SR, IN	4
Xysticus funestus Keys.	B	SC, SR, IN	5
X. ocala Gertsch	B	BT	1
X. discursans Keys.	B	SR	2
X. ferox (Hentz)	B	MS	1
Totals			65
Philodromidae			1
Tibellus maritimus (Menge)	B	MS	1
Totals			2
Salticidae			120
Ghelna sexmaculata (Banks)	B	SC, OL	2
Habrocestum xerophilum Richman	P, B	OC, SC, SF, MS, WS, SR, BT, OL, IN, JB, BS, SW	191
Habronattus alachua Griswold	P, F	MS, SR	3
H. notialis Griswold	B	BT	2
H. trimaculatus Bryant	B	SC	1
Maevia michelsoni (Walck.)	P, B, F	BS, SW	4
Marpissa lineata (CL Koch)	P	SF	3
M. dentoides Barnes	P	SC	1
Metacyrba taeniola (Hentz)	P	SF, MS, JB	3
Neonella vinnula Gertsch	P	JB	1
Pelegrina galathea (Walck.)	B	OL	1
Phlegra fasciata (Hahn)	P, B	OC, WS, SR	3
Phidippus regius CL Koch	B	OC	1
P. cardinalis (Hentz)	B	SR	1
Totals			337
Undetermined			22

domized sampling design (Steel & Torrie 1960). Point-centered quarter methodology was used to estimate frequency, density and basal area (cross-sectional area) of trees (30 sample points, 120 trees per study area) (Mueller-Dombois & Ellenberg 1974). Twenty points were selected at random and woody plants with stems less than 2.54 cm in diameter at 1.37 m above the ground were counted in plots (3 × 2 m) to provide density and frequency of shrubs. Two sides of the shrub plots were used to delimit line transects (5 m) to measure the canopy interception (%) of grasses and herbs. Because leaf litter was generally distributed over the study sites, it was selected to represent the horizontal and vertical variation in ground-level microhabitat available to spiders. Ten plots (0.1 m² each) were randomly positioned in the study areas and leaf litter was collected, oven dried, and the mass determined to the nearest gram. All measurements were taken once during the second year of study.

Data analysis.—Pearson correlation coefficient was used to test hypotheses concerning the relationship between spider abundance and ground level habitat features (SAS Institute 1990). A split-plot design for repeated measures ANOVA was used to test the hypothesis that no difference existed between spider abundance, richness (number of species), seasonality, and collection year (SAS Institute 1990). Three statistical terms used by Barnes & Barnes (1955) were calculated to compare the 20 most abundant spider species. First, presence is defined as the occurrence of a species in a particular stand without reference to its abundance or frequency: Site occurrence/total no. of sites × 100. Second, density is the average number of individuals of a species per sample. Third, frequency is the number of samples out of a possible 95 samples a particular species was taken. Similarity between the communities was determined using the Jaccard index of similarity:

$$IS_j = \frac{a}{a + b + c} \times 100$$

where IS_j = Index of Similarity, a is the number of species in common between communities A and B, b is the number of species unique to community B, and c is the number of species unique to community A (Krebs

1989). The range of the index is from 0 to 100.

RESULTS AND DISCUSSION

Biodiversity of ground surface spiders (n = 5236) in sandhill communities of north and central (peninsular) Florida was represented by 23 families, 92 genera, and 154 species (Table 1).

The number of species found for particular spider families ranged from 1–25. Linyphiidae had the richest representation with 16.1% of all species collected; however, among study sites, the family constituted from 1% (WS) to 62.8% (JB) of the species found in the individual collection sites. Numerically the family accounted for 2.2% of the total spiders collected.

Lycosidae made up the largest percentage of individual spiders collected (75.2%) and ranged from a low of 62.8% (JB, BS) to a high of 87.2% (WS) among sites (Table 1). A total of 21 species was collected, ranging from a minimum of 8 (SC, WS, IN) to a maximum of 11 (SR) among sites.

Lycosidae was followed in abundance by Salticidae (6.4%), Gnaphosidae (6.3%), Clubionidae (2.6%), Linyphiidae (2.2%), Theridiidae (1.5%), Thomisidae (1.2%) and Ctenizidae (1.0%) (Table 1). Linyphiidae was represented by the greatest number of species (25) followed by Lycosidae (21) and Gnaphosidae (21), Clubionidae (16), Salticidae (14), Theridiidae (13), Araneidae (7), Thomisidae (6), and Ctenizidae (5).

Only four species were collected at all 12 sites (presence of 100%, Table 2): the lycosids *Lycosa ammophila* Wallace 1942, *Schizocosa duplex* Chamberlin 1925, *S. segregata* Gertsch & Wallace 1937, and the salticid *Habrocestum xerophilum* Richman 1981. One additional species, *Castianeira descripta* (Hentz 1847), was present at 11 sites. Eighty-three (53.9%) of the 154 species were collected at only one site (Table 1).

Of the 20 most abundant species, 7 ranked in the top 10 for density, and 9 ranked in the top 10 for frequency (Table 2). *Lycosa ammophila, Schizocosa duplex,* and *Habrocestum xerophilum* were ranked 1, 2, 3 for presence, density, and frequency, respectively. *Schizocosa segregata,* although found at all 12 sites, ranked seventh in density and frequency. *Ozyptila floridana* Banks 1895, the

Table 2.—Presence, density, and frequency values for the twenty most abundant spider species collected in the Florida abstract sandhill community.

Species	Abundance Ranking	Presence (%)	Density	Frequency (%)
Lycosa ammophila	1	100.0	16.37	86.3
Schizocosa duplex	2	100.0	7.48	54.7
Habrocestum xerophilum	3	100.0	2.01	58.9
Lycosa carolinensis	4	75.0	1.12	35.8
Sosippus floridanus	5	75.0	0.98	34.7
Arctosa littoralis	6	58.3	0.85	23.2
Schizocosa segregata	7	100.0	0.78	29.5
Zelotes pseustes	8	58.3	0.57	32.6
Ozyptila floridana	9	41.7	0.49	9.5
Drassyllus aprilinus	10	66.7	0.46	18.9
Zelotes lymnophilus	11	66.7	0.44	14.7
Castianeira descripta	12	91.7	0.41	28.4
Talanites exlineae	13	83.3	0.39	18.9
Haplodrassus signifer	13	66.7	0.39	8.4
Gladicosa pulchra	13	75.0	0.39	14.7
Phrurotimpus minutus	16	33.3	0.29	6.3
Achaearanea porteri	17	58.3	0.27	16.8
Callilepis imbecilla	18	66.7	0.25	17.9
Rabidosa punctulata	18	41.7	0.25	7.4
Agelenopsis barrowsi	20	41.7	0.24	7.4

ninth most abundant species, was present at only five of the sites and had low density (0.49) and frequency values (9.5%).

Two new state records are reported: *Centromerus tennapax* (Barrows 1940) from Orange City and O'leno State Park, and *Tapinocyba hortensis* (Emerton 1924) from Morningside Nature Center and Starkey Well Field Area.

The 12 study sites were fairly dissimilar in species composition based on the Jaccard index of similarity ($\bar{x} = 26.1$; SD = 2.7). Spruce Creek Preserve and Interlachen were the most similar (39.6), followed by Spruce Creek Preserve and Boy Scout Reservation (38.8). San Felasco Hammock and Suwannee River State Park were the least similar (14.7) (Table 3). Corey & Taylor (1988) compared spider communities using Sorensen's index of similarity (Krebs 1989) and reported values of 0.65 (pond pine and flatwoods), 0.56 (sand pine scrub and flatwoods), and 0.51 (pond pine and sand pine scrub). Using Sorensen's index as a means of comparison, sandhill communities were dissimilar to Corey & Taylor's pond pine (0.20), sand pine scrub (0.18), and flatwoods (0.19). The high similarity values found by Corey & Taylor (1988) might have been due

to the close proximity of the three communities (all within 0.80 km of each other). The closest sandhill communities studied were approximately 8.5 km apart (BS and JB; $IS_j = 31.9$).

Foraging guilds of spiders in the sandhill community were derived from obvious behavioral modes (modified from Corey 1988; Bultman et al. 1982; Gertsch 1979). Guilds were: 1) sit and wait ambushers: Lycosidae, Pisauridae, Ctenidae, Heteropodidae, and Thomisidae; 2) active hunters: Gnaphosidae, Clubionidae, Oonopidae, and Salticidae; 3) aerial web spinners: Theridiidae, Araneidae, and Uloboridae; 4) ground level web builders: Agelenidae, Linyphiidae, Hahniidae, and Amaurobiidae; 5) all other families. Analysis of guild composition showed that all 12 sites were basically similar (Fig. 3). The sit and wait ambushers were the dominant guild on all 12 sites. Similar results were reported by Corey & Taylor (1988), Bultman et al. (1982), and Lowrie (1948). The sandhill communities were more heavily dominated by sit and wait ambusher spiders than were pond pine, sand pine scrub, and flatwoods communities, which had a more even distribution of guilds (Corey & Taylor 1988). Lycosidae have been found

Table 3.—Jaccard Index of Similarity for spider species collected in sandhill study sites of Florida. See text for site abbreviations.

	Collection Site										
	SC	SF	MS	WS	SR	BT	OL	IN	JB	BS	SW
OC	22.6	25.0	23.9	27.5	22.9	24.6	26.7	28.8	25.0	26.4	21.8
SC		19.0	21.9	21.2	23.5	25.9	20.0	39.6	25.9	38.8	23.1
SF			27.1	29.5	14.7	26.5	25.5	29.8	24.5	30.4	20.8
MS				22.8	22.7	31.6	26.6	29.3	31.0	25.0	37.7
WS					22.0	28.9	30.0	30.2	19.6	23.9	24.4
SR						19.4	17.6	28.3	21.9	23.4	18.6
BT							22.8	24.0	17.0	34.8	32.6
OL								19.6	24.5	18.6	24.1
IN									24.5	35.6	28.9
JB										31.9	27.7
BS											27.7

to occur in communities with little litter accumulation (Bultman et al. 1982), whereas thomisids and ground-level web builders (Agelenidae, Linyphiidae, and Hahniidae) increase in dominance as litter increases (Uetz 1979).

Pearson correlation coefficient was used to test the relationship between the abundance of the eight most common spider families collected and ground-level habitat features (SAS Institute 1990) (Table 4). The number of species and of individual spiders was not significantly correlated to any habitat feature ($P > 0.05$). Other studies have found correlations
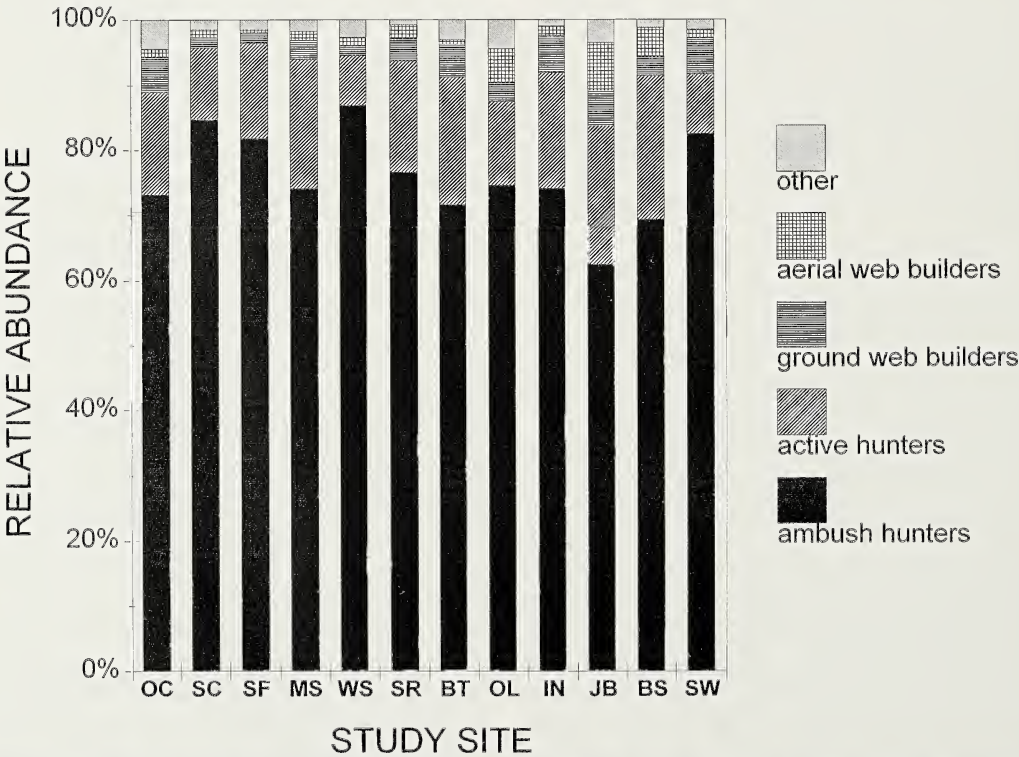

Figure 3.—Spider guild composition for 12 Florida sandhill study sites. See Figure 2 for site abbreviations.

Table 4.—Correlation (r) of the eight most common spider families abundance with ground level habitat features in Florida sandhills. + = for the entire sandhill population. * = r value significant at P < 0.05.

Family	Shrub density (No./m^2)	Grass-herb ground cover (cm)	Mass of plant litter (g)	Tree basal area (cm^2)
Lycosidae	−0.287	−0.001	0.079	−0.132
Thomisidae	0.660*	−0.013	−0.170	0.313
Linyphiidae	−0.166	0.241	0.088	−0.034
Gnaphosidae	0.172	−0.432	0.087	0.331
Clubionidae	0.264	−0.029	0.401	0.531
Theridiidae	0.522	0.190	−0.426	0.041
Salticidae	0.518	−0.201	0.106	0.689*
Ctenizidae	−0.229	0.447	−0.343	−0.680*
No. of species[+]	−0.272	−0.166	−0.110	−0.047
No. individuals[+]	0.488	0.069	0.039	0.452

between spider abundance and an increase in litter (Hagstrum 1970; Lowrie 1948). Thomisidae abundance was found to be significantly correlated ($P < 0.05$) to shrub density, and Salticidae abundance was significantly correlated to basal area of trees in the study sites. In contrast, Ctenizidae were significantly reduced in abundance on study sites with a high basal area of trees. Spider abundance in general was unrelated to or reduced by increased grass-herb ground cover (negative correlations in 6 of 10 comparisons, Table 4). These results suggest that the abundance of certain spider families is affected by the amount of incident sunlight received. Sites with a larger tree basal area would have more canopy cover and therefore create more shade than habitats with low basal areas.

Spider abundance ($F_{1, 22} = 2.56, P > 0.124$) and the number of species ($F_{1, 22} = 0.00, P > 0.952$) were not significantly different between the first and second years of collecting (Fig. 4). Based on the combined years, an analysis of split-plot design ANOVA (SAS Institute 1990) suggested that spider abundance ($F_{3, 66} = 6.17, P < 0.0009$) was significantly different among the four seasonal periods for the total sandhill population. Scheffe's test (a = 0.05) showed that winter, spring, and summer were not significantly different in total number of spiders caught. Likewise, fall and winter were not significantly different, but fall was significantly different from spring and summer. The number of species was also significantly different ($F_{3, 66} = 11.87, P <$ 0.0001) among the four seasons. Scheffe's test showed that spider populations in the fall were significantly different from spring and summer, and winter populations were significantly different from spring ($P < 0.05$). Other seasonal comparisons were not significantly different ($P > 0.05$).

Difference in the seasonal abundance of spiders was expected due to the variation in patterns of activity and mortality affecting adults and the appearance of juveniles. Indeed, variation in abundance of individual species between years one and two often accounted for observed seasonal differences at the study sites (Fig. 4).

Species observed to vary greatly from year to year at one site include: *Arctosa incerta* Bryant 1934, *Lycosa ammophila*, *Ozyptila floridana*, *Schizocosa duplex*, *Sosippus floridanus* Simon 1898, and *Zelotes pseustes* Chamberlin 1922. Some of the variation of *L. ammophila* (at SC and SW) was due to the capture of females with young (170 and 102, respectively).

Study sites appeared to be very similar in terms of soils, relief, drainage, and vegetal cover (Stout & Corey pers. obs.). Although guild structure was similar from site to site, the species composition of ground surface spiders showed a great deal of site variation. The substantial dissimilarity in the species composition of spiders from place to place in the remaining sandhill habitats suggests that conservation of spiders and, by inference, other invertebrate taxa of the ground surface fauna,
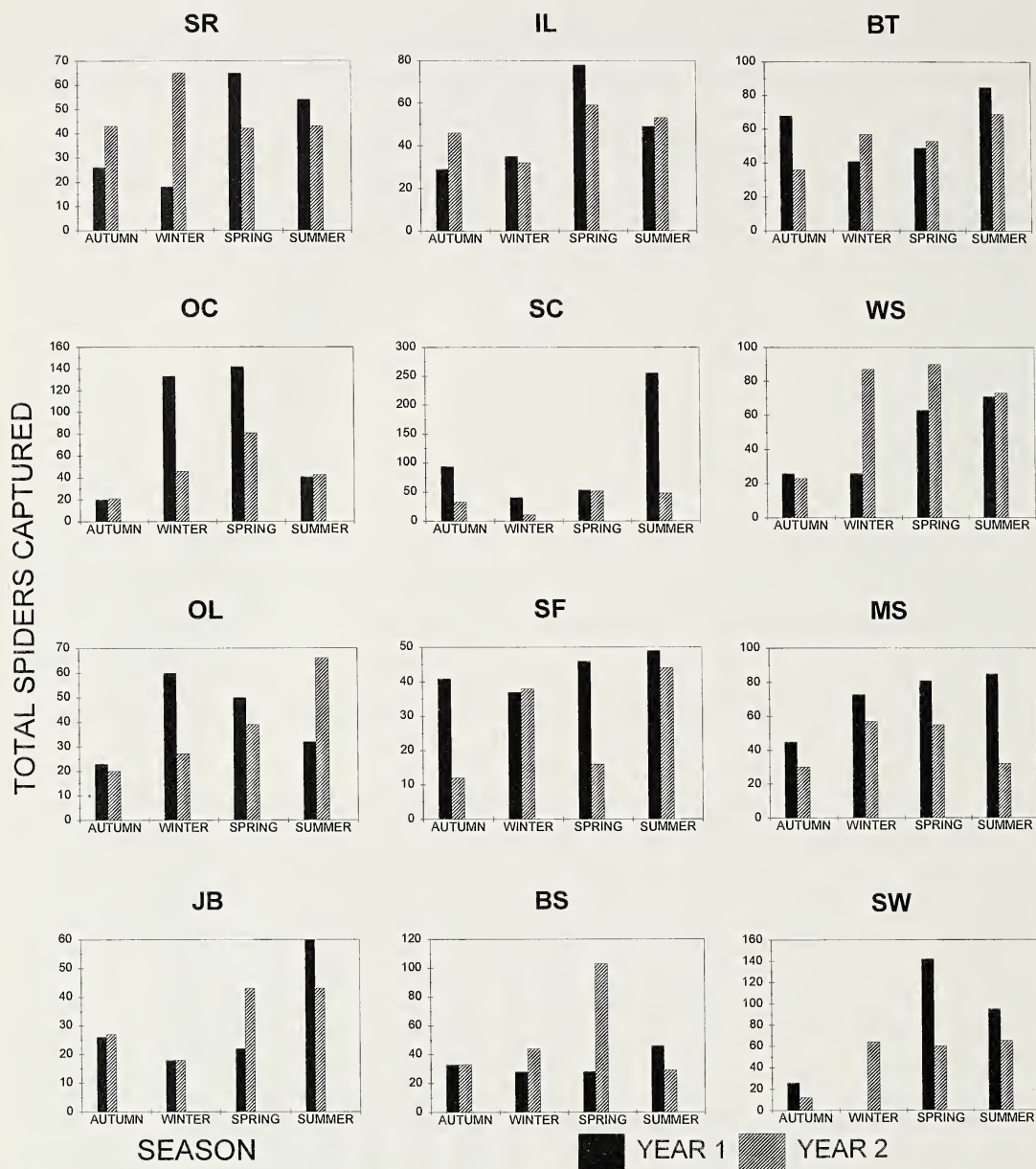
Figure 4.—Spider seasonal abundance in 12 Florida sandhill study sites. See Figure 2 for site abbreviations.

will require many sites to be preserved as opposed to a few larger sites (Main 1987).

LITERATURE CITED

Barnes, R.D. & B.M. Barnes. 1955. The spider population of the abstract broomsedge community of the southeastern Piedmont. Ecology, 36: 658–666.

Bultman, T.L., G.W. Uetz, A.R. Brady. 1982. A comparison of cursorial spider communities along a successional gradient. J. Arachnol., 10: 23–33.

Burgess, R.L. & D.M. Sharpe (eds.). 1981. Forest Island Dynamics in Man-dominated Landscapes. Springer-Verlag, New York.

Campbell, H.W. & S.P. Christman. 1982. Field techniques for herpetofaunal community analysis. Pp. 193–200. In Herpetological Communities (N.J. Scott, Jr., ed.). U.S. Fish and Wildlife Service, Wildlife Research Report 13.

Corey, D.T.& I.J Stout. 1990. Arachnid fauna in sandhill communities of Florida. J. Arachnol., 18:167–172.

Corey, D.T.& I.J. Stout. 1992. Centipede and millipede (Chilopoda and Diplopoda) faunas in sandhill communities of Florida. American Midl. Nat., 127:60–65.

Corey, D.T. & W.K. Taylor. 1987. Scorpion, pseudoscorpion, and opilionid faunas in three central Florida plant communities. Florida Sci., 50(3): 162–167.

Corey, D.T. & W.K. Taylor. 1988. Ground surface spiders in three central Florida plant communities. J. Arachnol., 16:213–221.

Corey, D.T. & W.K. Taylor. 1989. Foliage-dwelling spiders in three central Florida plant communities. J. Arachnol., 17:97–106.

Cox, J., R. Kautz, M. MacLaughlin & T. Gilbert. 1994. Closing the gaps in Florida's wildlife habitat conservation system. Office of Environmental Services, Florida Game and Fresh Water Fish Commission, Tallahassee.

Davis, J.H. 1980. General map of natural vegetation of Florida Agr. Exp. Sta., Inst. Food and Agr. Sci. Circular S-178. University of Florida, Gainesville.

Gertsch, W.J. 1979. American Spiders. 2nd ed. Van Nostrand Reinhold Co., New York.

Hagstrum, D.W. 1970. Ecological energetics of the spider Tarentula kochi. Ann. Entomol. Soc. America, 63:1297–1304.

Harper, R.M. 1927. Natural resources of southern Florida. Pp. 27–192. In 18th Annual Report of the Florida State Geological Survey. Tallahassee.

Krebs, C.J. 1989. Ecological Methodology. Harper & Row, Publishers, Inc., New York.

Laessle, A.M. 1942. The plant communities of the Welaka Area. Univ. of Florida Publ., Biol. Sci. Series 4:1–143.

Laessle, A.M. 1958. The origin and successional relationship of sandhill vegetation and sand-pine scrub. Ecol. Monogr., 28:361–387.

Lowrie, D.C. 1948. The ecological succession of spiders of the Chicago area dunes. Ecology, 29: 334-351.

Lowrie, D.C. 1963. The effects of grazing and intensive collecting on a population of the green lynx spider. Ecology, 44:777–781.

Lowrie, D.C. 1971. Effects of time of day and weather on spider catches with a sweep net. Ecology, 52:348–351.

Main, B.Y. 1987. Persistence of invertebrates in small areas: Case studies of trapdoor spiders in western Australia. Pp. 29–39. In Nature Conservation: The role of Remnants of Native Vegetation (D.A. Saunders, G.W. Arnold, A.A. Burbidge, & A.J.M. Hopkins, eds.). Surrey Beatty & Sons Pty. Limited, in asso. with CSIRO and CALM.

Mueller-Dombois, D. & H. Ellenberg. 1974. Aims and Methods of Vegetation Ecology. John Wiley & Sons, New York.

Muma, M.H. 1973. Comparison of ground surface spiders in four Central Florida ecosystems. Florida Entomol., 56:173–196.

Muma, M.H. 1975. Spiders in Florida citrus groves. Florida Entomol., 58:83–90.

Myers, R.L. 1985. Fire and the dynamic relationship between Florida sandhill and sand pine scrub vegetation. Bull. Torrey Bot. Club, 112: 241–252.

Myers, R.L. 1990. Scrub and high pine. Pp. 150–193. In Ecosystems of Florida. (R.L. Myers & J.J. Ewel, eds.). Univ. of Central Florida Press, Orlando.

Post, W.M., III & S.E. Riechert. 1977. Initial investigation into the structure of spider communities. J. Anim. Ecol., 46:729–749.

Platt, W.J., G.W. Evans & M.M. Davis. 1988. Effects of fire season on flowering of forbs and

shrubs in longleaf pine forests. Oecologia, 76: 353–363.

Rey, J.R. & E.D. McCoy. 1983. Terrestrial arthropods of Northwest Florida salt marshes: Araneae and Pseudoscorpiones (Arachnida). Florida Entomol., 66:497–503.

SAS Institute. 1990. User's Guide: Statistics, Version 6 Ed. SAS Institute, Cary, North Carolina.

Saunders, D.A., R.J. Hobbs & C.R. Margules. 1991. Biological consequences of ecosystem-fragmentation: a review. Conser. Biol., 5:18–32.

Steel, R.G.D. & J.H. Torrie. 1960. Principles and Procedures of Statistics. McGraw-Hill Book Co., Inc., New York. 481 pp.

Stout, I.J. & W.R. Marion. 1993. Pine flatwoods and xeric pine forests of the southern (lower) coastal plain. Pp. 373–446. *In* Biodiversity of the Southeastern United States (W.H. Martin et al., eds.). John Wiley and Sons, Inc., New York.

Uetz, G.W. 1979. The influence of variation in litter habitats on spider communities. Oecologia, 40:29–42.

Wells, B.W. & I.V. Shunk. 1931. The vegetation and habitat factors of the coarser sands of the North Carolina coastal plain: an ecological study. Ecol. Monog., 1:465–520.

Whitcomb, R.F. 1987. North American forests and grasslands: biotic conservation. Pp. 163–176. *In* Nature Conservation: The Role of Remnants of Native Vegetation (D.A. Saunders et al., eds.). Surrey Beatty & Sons Pty. Ltd., in asso. with CSIRO and CALM.

Wilcove, D.S., C.H. McLellan & A.P. Dobson. 1986. Habitat fragmentation in the temperate zone. Pp. 237–256. *In* Conservation Biology (M.E. Soulé, ed.). Sinauer Associates, Inc. Sunderland.

BEHAVIOR, LIFE CYCLE AND WEBS OF
MECICOBOTHRIUM THORELLI
(ARANEAE, MYGALOMORPHAE, MECICOBOTHRIIDAE)

Fernando G. Costa and Fernando Pérez-Miles: División Zoología Experimental, Instituto de Investigaciones Biológicas Clemente Estable, Av. Italia 3318, Montevideo, Uruguay

ABSTRACT. A comprehensive study of the biology of *Mecicobothrium thorelli* Holmberg 1882 was carried out in the laboratory and in the field (Sierra de Animas, Maldonado, Uruguay). The species is found in shady riparian sites under trees. *M. thorelli* builds sheet-and-funnel webs under stones, logs, roots and in crevices. In the laboratory, developmental data indicated that the spiders have an inactive phase in summer and probably another in winter. Adults emerged in the fall and the males die during late winter. Three egg-clutches of about 30 eggs were observed in the laboratory at the end of winter and the beginning of spring (August-September). Juveniles emerged from one of the clutches 27 days after oviposition. A three-year lifespan was estimated. Males started courtship (body vibrations and palpal drumming) upon contacting the female web. Females showed high tolerance during the entire sexual interaction. An unusual clasping mechanism was observed before and during copulation: the female engaged her cheliceral fangs into grooves on the male chelicerae. Twenty-eight copulations were observed. Mean copulation duration was 24.7 min, while males performed a mean of 10 alternate palpal insertions. The complex insertion pattern is described and analyzed. Half of the copulated males pursued females after uncoupling. These males expelled females from the web and remained there. Mated males aggressively defended the female's web from other males. The reproductive strategy, cheliceral clasping and palpal insertion pattern are discussed in detail. Phylogeny and biogeography of mecicobothriid genera are also considered.

The family Mecicobothriidae was established by Holmberg (1882) to include small-sized mygalomorphs found in Argentina. These spiders have unique morphological features (abdominal tergal plates, longitudinal fovea and elongated posterior lateral spinnerets). Mecicobothriid monophyly was supported by Gertsch & Platnick (1979) and by Raven (1985). Recently, Goloboff (1993) placed Mecicobothiidae as a sister group of the non-atypoid Mygalomorphae. Following Barrowclough (1992) this characteristic justifies giving high priority to the conservation of the Mecicobothriidae, considering the importance of this family to studies of spider phylogeny. The geographic distribution is also crucial because these spiders are only known from temperate regions of North and South America.

Mecicobothrium thorelli Holmberg 1882 (Figs. 1, 2) is the only mecicobothriid known from the Southern Hemisphere. It was originally recorded from Argentina (Buenos Aires: Tandil, Balcarce and Sierra de la Ventana (Gertsch & Platnick 1979)) and Uruguay (Maldonado, Sierra de las Animas (Capocasale et al. 1989)). Other Mecicobothriidae occur only in North America. Biological data on North American mecicobothiid species were given by Gertsch & Platnick (1979). *M. thorelli* was found in Uruguay in hilly zones in riparian woods under stones, roots and trunks, and in holes in the tree bases (Costa et al. 1991; Pérez-Miles et al. 1993). Lack of knowledge of the biology of this group, together with the presence of enigmatic cheliceral male apophyses, challenged us to conduct field and laboratory studies on the biology of *M. thorelli*.

Our objective was to describe and analyze the development, life cycle, phenology, webs and, especially, the sexual behavior of *M. thorelli*. This last aspect, poorly known in Mygalomorphae, is unknown in Mecicobothriidae.

METHODS

Specimens of *M. thorelli* were collected at Sierra de las Animas, Maldonado, Uruguay, in

Figures 1–3.—*Mecicobothrium thorelli.* 1, Adult male; 2, Adult female; 3, Sheet and entrances of *M. thorelli* web in the laboratory. (Photos by M. Lalinde).

the streamside forest of Pedregoso Stream (34°45′S, 55°15′W). The cryptozoic arachnofauna of this site has been intensely studied (Capocasale et al. 1989; Costa et al. 1991; Pérez-Miles et al. 1993; Capocasale & Gudynas 1993; Costa & Pérez-Miles 1994). Voucher specimens were deposited in the arachnological collection of the Museo Nacional de Historia Natural, Montevideo.

Six field collections were made: 1) 4 females, 2 males and 5 juveniles on 29 June 1989; 2) 1 female and 9 juveniles on 16 August 1989; 3) 3 juveniles on 20 November 1989; 4) 3 females, 1 male, 5 juveniles on 18/19 May 1990; 5) 33 juveniles on 9 September 1994; and 6) 36 juveniles on 21 September 1995. Individuals from the last collection were measured and released, except six which were raised. Silk constructions were observed in the field. On 30 June 1993, measurements were made of 17 webs of *M. thorelli,* the stones that covered them, and the distances to the stream (spiders were not collected).

Seventy-two individuals were kept in the laboratory from June 1989–April 1996. Most individuals were placed in glass vials of 80 mm $\times$ 15 mm, with damp cotton wool at the bottom end and dry cotton wool closing the open end, leaving 5 cm of free space in the vial for the spider. Vials were maintained slightly inclined with the open end upward. For specific observations and for short periods spiders were maintained in: a) glass jars of 9 cm diameter, with soil, water provision and a microslide covered with a plumb bob. Under the microslide we made a small burrow to facilitate spider excavation. Plumb bob removal allowed us to observe the spider. b) Arena A. Petri dishes of 9 cm diameter with a damp cotton wool placed centrally and a small vial (30 mm $\times$ 7 mm) with both ends open, placed against the dish wall. c) Arena B. Cylindrical glass jars of 14 cm diameter, with soil, water and a piece of wood of 3 cm diameter placed on the soil. We made a small burrow under the wood to facilitate spider excavation.

The temperature in the laboratory varied with the outdoor temperature, except in winter when it was maintained around 20 °C (range: 15–23 °C). Natural light was provided by windows facing west; artificial light was on from Monday to Friday from 0830 to 1700 h. Spiders were fed mainly with *Tenebrio* sp. larvae

(alive or in pieces), sometimes complemented by flies, mosquitoes, small beetles, silverfish, etc.

Thirty male-female encounters were set up with 32 of the spiders collected on 9 September 1994. Twenty observations of these encounters occurred in a female breeding vial connected to an open petri dish (9 cm diameter), containing sand and surrounded with a plastic band 45 mm high (Arena C). The entrance (2 cm) of the female's glass tube had no silk because the cotton wool plug was removed before the encounter. Arena C was elevated in such a way that observations could be made from below using a 5× lens and focused light. Six observations were done in Arena A and the other four in Arena B. All available males and females were used. Observations were carried out between 9 May–3 July 1995 (fall/winter). Laboratory temperature varied between 16 and 24 °C; observations were conducted at 22.2 ±1.1 °C (range: 19–23.5 °C). Other male-female encounters, including a copulation, were recorded on Super-8 movie film.

RESULTS

Webs and retreats.—The spiders construct dense funnel-and-sheet webs (see Coyle's 1986a nomenclature). The web, after experimental wetting, appeared to be hydrophobic. The distance from the web to stream edge for seven individuals was 5.28 ±4.55 m (range 0.57–10 m). The web nearest the stream was found at 25 cm above the water level. Presumably the spiders remain in the retreats during short-term rain-caused flooding. In the laboratory, we observed that they easily drown in a fine water film if webs are lacking. Two of 17 webs observed in the field were not occupied; no male was observed occupying a complete web.

The funnel (tubular retreat) of the web extends under the stone (or similar object) and emerges with one or more entrances onto a small, irregular prey capture sheet (Fig. 3). In the field, this sheet lies on the soil, extends to both sides of the entrances, and continues beneath the leaf litter, moss or grass. Retreat tubes were more or less curved, some of them branched. Seven webs had only one entrance, two webs had three entrances, and one had four entrances. Eight webs were found under stones and one was under a log. Stones with

webs measured 225 ±101 mm long, 168 ±59 mm wide and 103 ±33 mm high. The mean major axis of the silk tubes was 64 ±20 mm and their diameter varied from 4–8 mm. A web constructed in the laboratory by an adult female consisted of two more-or-less parallel tubes fused medially (H-shaped web): its total length was 23 mm, the exposed portion lying on the soil was 14 mm, and the underground portion was 9 mm. This web was constructed under a small section of a branch placed on the soil.

Females which copulated in the laboratory and lived in glass vials exhibited reduced web construction in winter. Eight females placed in containers with soil each occupied a burrow made for it under a piece of glass. These females did not make webs but excavated and closed the burrow entrance with soil and silk. Usually males made a silk mat in the glass vials during winter, but only one male made a rudimentary retreat. Males placed in containers with soil similar to those used for females rarely occupied pre-existing burrows.

Prey capture.—When a prey is offered, the spider detects vibrations through the web and suddenly approaches the prey, biting it and pulling it back to the retreat, entangling the prey with silk threads while it is being carried. Adult males also fed actively.

Daily activity pattern.—Spiders in the laboratory showed little diurnal activity. When a light was turned on in the dark winter mornings, spiders ran back into their retreats. The dense draglines observed around the inner periphery of the containers suggested they were very active during night.

Development and reproduction.—Thirty-three large juveniles were captured on 9 September 1994. No subadult individuals were found then. The spiders constructed the retreat in the damp end of the glass vial; each retreat had two lateral entrances. One animal died 29 days after capture. The 32 remaining individuals matured in the laboratory (19♂13♀). Seasonal distribution of the molts is given in Fig. 4. These spiders molted synchronously at the beginning of October. Between October and December they molted an average of 1.5 ±0.6 times. Smaller animals molted more frequently than larger ones. In the warm period (last three weeks of January and first two of February) no molting occurred. Molting resumed at the end of February and continued
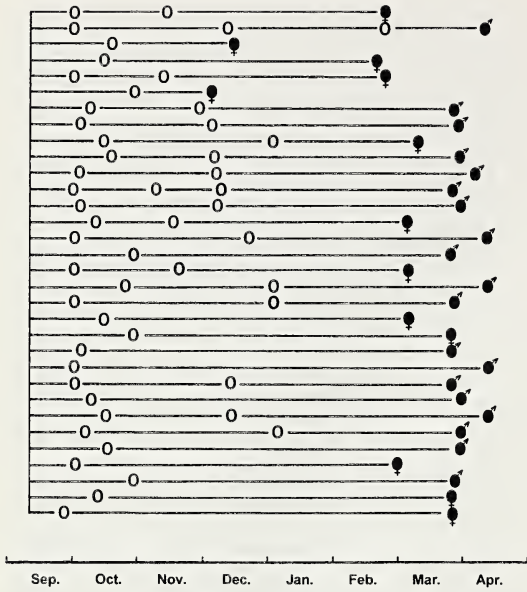
Figure 4.—Development of 32 juveniles collected on September 9, 1994. Empty circles (○) indicate ordinary molts and dark circles (●) indicate the maturation molt and sex.

to April, when all individuals had reached maturity. The spiders carried the exuviae far away from the retreat.

Male palpal tarsi were incrassate in the penultimate instar. No evidence of spermathecae was observed in the last exuviae of females. Females molted over a longer period (December–March) and earlier than the males. Males

reached maturity in a very limited period (last week of March and first two weeks of April) (Fig. 4). The time of maturation molts of both sexes overlapped only in the last week of March. Laboratory rearing showed that males molted (2.79 ±0.63 times) more times than did the females (2.38 ±0.51 times), with significant differences in the Mann-Whitney's U-test ($U = 77.5$, $P < 0.05$).

Adults mated in the laboratory from 9 May–3 July 1995. Two males died accidentally (bad manipulation) after the copulation. Males lived 118–206 days ($\bar{x} = 166.5$ ±22.9 days, $n = 16$) and females lived 161–298 days ($\bar{x} = 215.5$ ±41.4 days, $n = 12$) after reaching adulthood. The male and female adult lifespans were significantly different (Student's t-test; $t = 3.84$; $P < 0.001$).

Complementary results were obtained from five other groups that were reared between 1989–1996 and kept under conditions similar to the previous described group. Molts started in August and were especially frequent in September-December and March-April (Fig. 5). Molts were very rare or absent in June-July and January-February. Maturity molts were frequent in March and April. Two exceptional maturity molts were observed, an early male (February) and a late male (May, dead when molting). Six males raised in the laboratory lived 172.2 ±19.7 days after maturity. Another male captured as adult lived 160 days. Two females molted in March and lived as adults 206 and 393 days, respectively.
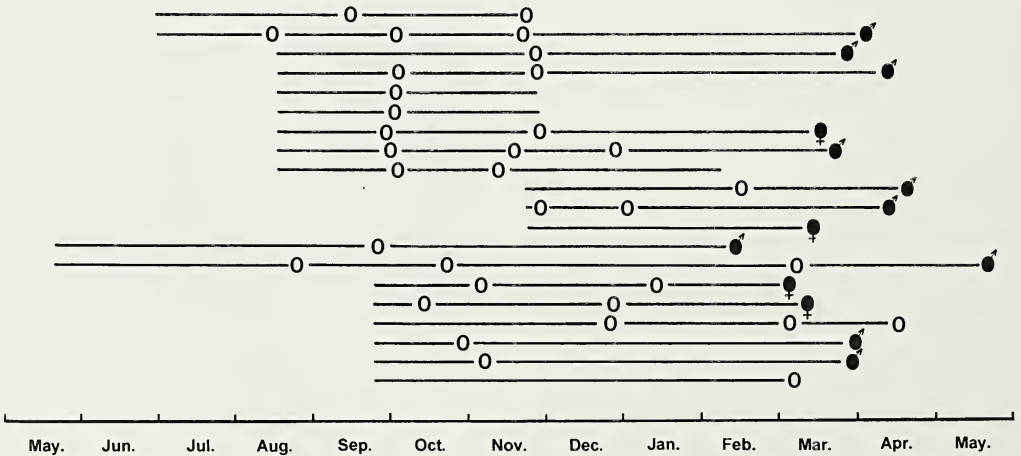

Figure 5.—Development of five groups of *M. thorelli* from five collections. Empty circles (○) indicate ordinary molts and dark circles (●) indicate the maturation molt and sex. Some of these juveniles did not reach maturity due to natural or accidental death, or were sacrificed.
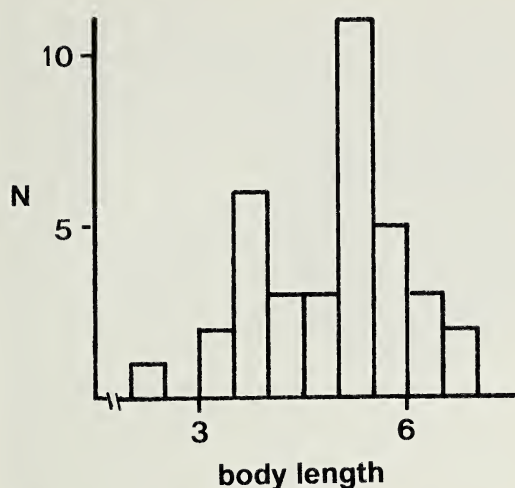
Figure 6.—Body length (in mm) distribution of a sample of 36 individuals of *M. thorelli* collected on 21 September 1995 in Sierra de las Animas, Maldonado. Class intervals: 0.5 mm, N: absolute frequencies.

On 21 September 1995, 36 individuals (no adults or subadults) were captured, and most of them were released after being measured. Six were reared in the laboratory. Measurements of these six were made from successive molts. Body size distribution is shown in Fig. 6. Carapace length increased between 9.4 and 22.0% during the molt ($\bar{x} = 15.5 \pm 3.4\%$, $n = 14$). The relative size increase was not related to the size of the individual. Small spiders (less than 3 mm body length) are very light brown while large juveniles are darker. The abdomen of some adult females becomes lighter when swollen.

In the laboratory males had their maturation molt between February and May, with a clear peak between March and April (Figs. 4, 5). Adult males lived from February to October. An egg-clutch was observed in the laboratory on 27 September 1989, from a female collected on 16 August. In the retreat, the eggs were agglomerated in a sphere without a well-developed silk cover, resembling the egg-sac of *Pholcus phalangioides* (Fuesslin 1775). The egg-sac, slightly larger than the carapace of the female, contained 33 yellow, translucent eggs. The female kept the egg-sac until the emergence of the spiderlings, 27 days after oviposition. The female died on 9 January 1990. Two other egg-sacs were observed in the laboratory on 31 August: one of them was eaten immediately by the female, the other contained 26 eggs (all of which were dead and decomposed) when the female died.

Courtship.—In Arena C, males were placed on clean sand and they walked to enter the female's glass vial. A rim of female silk was observed when the cotton plug was removed. Thirteen of 20 males stopped on the silk rim, remained immobile between 4–128 sec, and then started sexual activity. The other seven males began sexual activity just inside the female's web. In Arena B, males walked around the periphery of the arena (on female draglines) but initiated their sexual behavior only very close to the female's retreat. Finally, in Arena A, sexual behavior started close to the small glass vial where the female resided, or after female contact.

Male sexual behavioral units elicited by the female web were: 1) Body vibrations, which are brief, rapid, sagittally orientated body movements, and are apparently caused by leg-III movements. 2) Palpal drumming, which are alternate movements of palps against the substratum; these movements turn into steps when the male walks. 3) Leg tapping, in which the forelegs touch the female's silk mat, pulling the silk and sometimes penetrating it. These units took place alone or during slow locomotion movements and were interrupted by brief motionless periods. The main behavioral sequence was locomotion with body vibrations at the beginning, with leg tapping and palpal drumming added later. Similar behavior was observed in eight males which contacted the silk of females which had been removed from their breeding containers. This first searching phase lasted from 17 seconds to 22 minutes, until the female was contacted. Females did not attack or approach the males but remained immobile or retreated. After making direct contact, the male increased his tapping movements on the female body and legs. The male penetrated the silk and oriented toward the female chelicerae. Then the male pushed the female with his chelicerae. His cephalic region was directed downward while pushing her and his legs I and II held the female, preventing upward biting (Fig. 7). The male exerted a great effort to maintain this frontal position with respect to the female. Females were passive and generally flexed their legs against their bodies.

Males pursued females sometimes with ap-
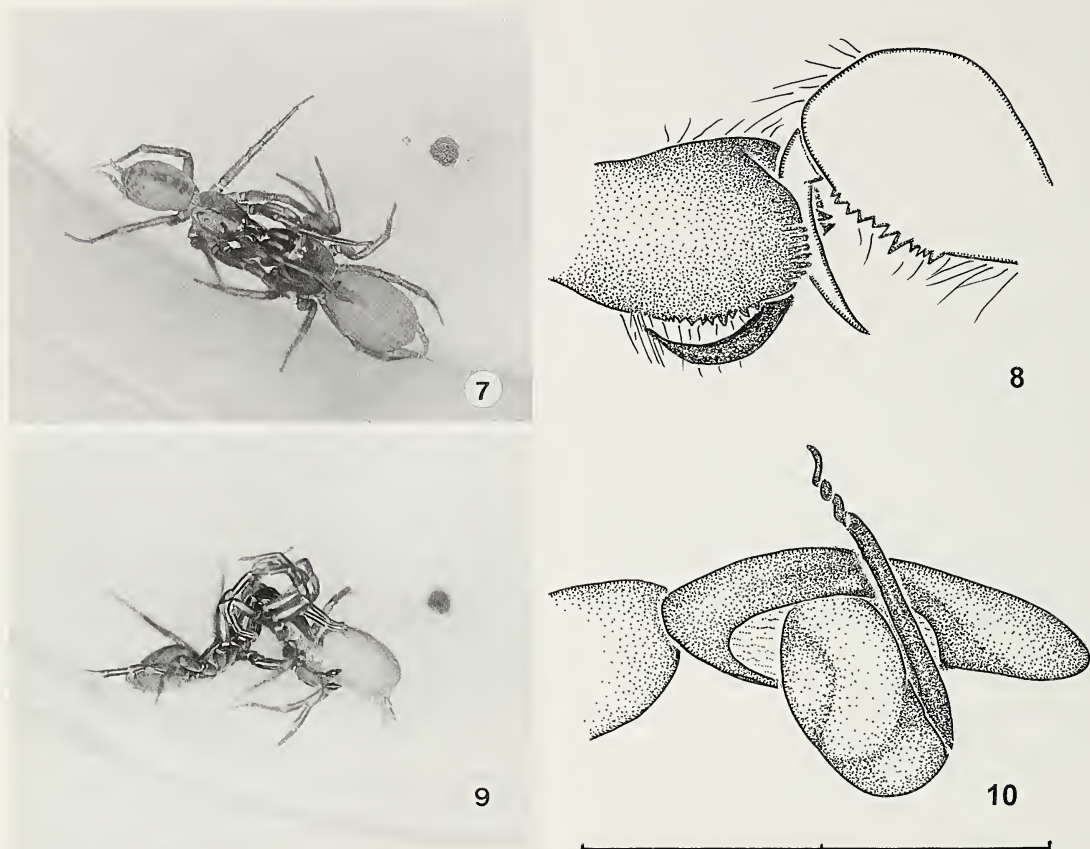
Figures 7–10.—Copulation in *Mecicobothrium thorelli*. 7, Initial stage of copulation. Male (at left) pushing female with his chelicerae while legs I and II prevent upward biting; 8, Schematic representation of the cheliceral clasping, prolateral view. Female fang (to the right) penetrates into the male cheliceral groove delimited by two apophyses and several cusps; 9, Copulation and palpal insertion. Cheliceral clasping and legs I and II of the male (at left) firmly maintain this position. The long palps of the male are able to reach the female genital zone without extreme elevation of the couple; 10, Embolus position during insertion attempt of male right palp, reproduced from a preserved specimen. (Photos M. Lalinde)

parent violence. The male usually spread apart his chelicerae when pushing the female, but he never attempted to bite her. This sequence was repeated until the female finally opened her chelicerae and bit into the male's cheliceral groove lying between the two cheliceral apophyses. Her fangs remained firmly between these cheliceral apophyses (Fig. 8). During cheliceral clasping, the male performed rough up-and-down movements. Hinge-like body movements were performed 3–7 times, while pulling the female backwards. If the female was small or showed low resistence, the male pulled the female out of the retreat and copulation took place on the sheet-web. Otherwise, the male pulled the female to near the entrance. The duration from

beginning contact with the female to the completion of clasping varied from 10 sec to 8.5 minutes.

Copulation.—Twenty-six copulations were observed. Copulation can occur completely inside the retreat. Cheliceral clasping and the long male palps allowed a non-elevated copulation position, which took place in the narrow silk tube. The ventral angle between longitudinal body axes was 90° (if male is small) or more. Also, the cephalothorax and abdomen can adopt a small dorsal angle to facilitate mating in small spaces. Females were extremely passive during copulation. However, when one copulating male was intentionally disturbed for photographic purposes, the female attacked and killed him. Later the same

day, the same female copulated normally with another male. In another encounter, the couple had difficulty in uncoupling: the male remained entangled in the web after being released. The female then attacked and killed him.

During copulation (Fig. 9), the male-female ventral body angle varied (according to spider size) between 90–130°. The female's legs I and II were flexed against her body. The male placed his forelegs dorsally on the female, legs II more laterally, with legs III and IV on the floor, maintaining the equilibrium. Male palps were extended to the female venter during copulation (Fig. 9). That the male palpal femora and tibiae are bent dorsally was evident during insertion.

The palpal insertion pattern was complex. The embolus reached a perpendicular position with respect to the dorsum of the palp, but turned slightly back to be inserted (Fig. 10). Embolus movement was reconstructed in dead specimens under the stereo-microscope. The palpal bulb rotated around an approximately dorso-ventral axis of the palpal tarsus. The palpal embolus emerged retrolaterally, moving along the glabrous notch and stopping in a small retrolateral lobe (see Gertsch & Platnick 1979, figs. 46, 47, 50). Palpal bulb rotation was complex. Initially the tip of the embolus turned retrolaterally and later went upward; it is possible that the whole palp also rotates. When manipulated in preserved specimens, the embolus is flexible. In resting position the palpal embolus is prolateral and parallel to the longitudinal axis of the palpal tarsus, its tip points forward, and it is protected by a wide notch and a prolateral paracymbium-like lobe.

During copulation the palpal tarsus approached the epigastric furrow, which appeared swollen. The embolus was inserted and, in this position, insertion/withdrawal movements were repeated numerous times. These movements were generated by the tibio-tarsal joint of the palp. Withdrawal movements were discontinuous, suggesting that they must overcome a mechanical resistence. Discontinuous female abdominal movements were also observed synchronously. During withdrawal movements the palpal tarsus reached a dorsal angle of nearly 90° with respect to the tibia. Finally, the palp remained immobile in the insertion position. Only the

corkscrew-shaped portion of the embolus penetrated during insertion, the straight basal portion remained visible. We attempted to reconstruct the insertion with dead specimens and observed that only the right embolus can enter the right receptacle (and the same for left organs) according to the complementary spiral orientation. During the insertion of one palp the other remained extended, either moving or being immobile against the female abdomen. The embolus extraction was similar to insertion-withdrawal movements, pivoting on tibio-palpal joint. Despite the difficult observation of small spiders through the dense webs, the insertion pattern was clearly seen in 12 copulations and partially observed in another 4.

During early palpal insertions, the in-out movements were frequent. Males performed three, four, five or more insertion-withdrawal movements during a period of 1–6 min. The palps did not always alternate; two–four successive insertions with the same palp were common, especially following a failed insertion attempt.

Males performed 2–22 ($\bar{x}$ = 10.3 ±6.5, n = 10) palpal insertions during a period of 5.7–30.0 min ($\bar{x}$ = 18.4 ±8.6 min). Late insertions were brief (10–40 sec) and involve in-out movements only during palpal extraction. Other behaviors present in the periods between insertion attempts increased in frequency during the later stages of copulation. These behaviors were: pulling of male and female, moving outside and inside the retreat; rearrangement of legs; hinge-like movements (when the angle between the bodies changes); leg push from male to female, etc.

During the 26 copulations observed, only two pairs reclasped after unclasping. Unclasping had complications. The male pulled and/or pushed the female, forcing her outside the retreat and pulling her with his legs. The most conspicuous maneuvers of the male were cheliceral outspreading as well as series of violent hinge-like movements. The female allowed unclasping and determined the end of the copulation. When females did not release the male chelicerae, additional insertions could occur. An extreme case was a male which attempted to unclasp after 35 min of copulation but the female kept him in the copulation position for 21.5 min more. In another remarkable case the female dragged along the

male (for 32 min) because one fang remained clasped. This long interaction ended when the male unclasped (at 120 min) and the female killed him. Cheliceral anomalies were not found in these specimens.

Copulation duration from the start of clasping to complete unclasping was 11–56.5 min ($\bar{x}$ = 24.7 ±10.0, n = 23). Three other copulations were unusual. Two of these pairs unclasped and clasped again: one unclasped at 19 min, clasped again after 3 min and continued copulating for 18 min; the other unclasped at 14.5 min, clasped again after 3 min and then definitively unclasped without inserting, after 2 min. The third case was described above and involved the most difficult unclasping, which lasted 88 min.

All available individuals in the laboratory copulated (18♂, 13♀). In some cases copulation did not occur during the first encounter, but only after a second (two cases) or third attempt (one case). Failed attempts were one with a virgin female and three with once-mated females. Eight males recopulated between 8–47 days after first copulation. Twelve females (one female died after first copulation) recopulated between 5–44 days after first copulation; one female made a third copulation 12 days after the second copulation.

Postcopulatory activities.—Thirteen males were very active after copulation. These activities included leg tapping, violent pushes with outspread chelicerae, and conspicuous body vibrations when males pursued females. Females hid in the retreat and remained very passive. In response to these male behaviors, females flexed their legs against the body and remained immobile (with venter up in two cases). These males continued pursuing the female until the female abandoned her web. If the female returned, the male pursued her again until she remained outside the web. These males then took over the female webs, occupying the retreat. In other cases the males touched the female, made palpal drumming and slightly pushed her. In four encounters the male remained peacefully in the retreat with the female for 30 min, at which time he was removed. In three encounters the female left the web and came back several times, without being disturbed by the male. In another three encounters, males ran away from the web after copulation. Finally, in two encounters both partners ran away after copulation and in one

encounter the female killed the male after a difficult uncoupling.

In four encounters carried out in Arena B, with a more complex web, the female retreated to the bottom of the funnel. Although the males persisted, only one female left the web. In the other three encounters the male stayed together with the female for at least 30 min. These males placed themselves at the entrance of the funnel web and sporadically contacted the female; but no attacks were observed. Later, another male (intruder) was placed in each of these three webs which the males were guarding. These intruders began to court as soon as they touched the web near the entrance. Then the guarding male vigorously attacked the intruder. In one case the intruder won; the guarding males won the other two contests. In one of these last two encounters the fight was long; the males fought in a ritualized manner, pushing themselves with outspread chelicerae, which resemble a rhomboid from the dorsal view. With legs I and II firmly interlaced, the males bit the web several times. After a separation, one male caught the other from behind but did not bite him; when the first turned around they re-initiated the frontal embrace. Guarding winners touched the females and returned to guarding. The intruder winner unsuccessfully courted the female. No spiders were damaged. Males were removed between 30–60 min after copulation.

Two other copulations, one partially recorded in a Super-8 movie-film, were observed in 1990, using Arena A. Courtships and copulations were similar to those previously described and copulation durations were 24.5 and 55 min.

DISCUSSION

Habitat and webs.—The high sensivity of *M. thorelli* to humidity variations seems to be critical in understanding its biology and ecology. In the laboratory, individuals not provided with abundant water quickly died, but a minimal excess of water also caused the death. This sensivity clearly suggest a high dependence on the funnel-and-sheet web. The need for hygro-thermo stability is also emphasized by reinforced by their habit of living under stones, roots and trunks, in hilly areas in streamside forests. Probably the web gives protection from desiccation and occasional flooding. Although this species lives near the

water it does not invade the stones of the dry stream bed (Costa et al. 1991; Pérez-Miles et al. 1993). Then, *M. thorelli* seems to be very restrictive in its habitat selection. Collection data from Argentina, Provincia de Buenos Aires, generally agree with our findings (Holmberg 1882; Goloboff & Ramírez 1991; Maury *in litt.*). Also, North American Mecicobothiidae live under stones or other objects in the soil, in crevices, and deep in organic ground litter (Gertsch & Platnick 1979). These species are frequently found in the shade of coniferous and oak woods from Washington and Oregon to California (western USA).

Our observations indicate that adult males do not construct funnel-and-sheet webs, but Holmberg (1882) found the holotype male in a funnel web of 2 cm length which opened onto a sheet of 2 cm². Holmberg was not sure if the male was occupying its own web because he found several individuals of "*Tegeneria*" in coexistence. *M. thorelli* found in Sierra de las Animas were syntopic with hydrophilic spiders of the genus *Diapontia* (Lycosidae), the webs of which could correspond to Holmberg's "*Tegenaria*". However, it is more likely that the male collected by Holmberg was occupying a conspecific female web; this would fit our observations of postcopulatory female expulsion. Or perhaps this male had recently molted to adulthood in his juvenile web.

Apart from the role of webs in water regulation, they also play a key role in prey capture. *M. thorelli* has long posterior spinnerets well suited for sheet-web construction and repair. Biting and pulling back behavior in prey capture is widely distributed among spider taxa, suggesting a primitive condition. This technique is simple and safe because entangled threads effectively prevent the defensive movements of the prey. North American Mecicobothriidae also live in funnel-and-sheet webs and show similar prey capture tactics (Gertsch & Platnick 1979).

Life cycle.—Most spiders collected in September 1994 molted in October 1994 (Fig. 4). This synchronized development would reflect the influence of uniform breeding conditions, mainly feeding. These juveniles molted 2, 3 or 4 times to reach maturity. Therefore, maturity molting seems to occur in a fixed period of the year, independent of the initial developmental stage. Two main factors seem to determine the time when the spider will molt to maturity: biorhythm and seasonal environmental factors. Females reach maturity before males, which explains why males molt more times than females during September–April. Females of *Hypochilus pococki* Platnick 1987 (Hypochilidae) also reach maturity earlier than males (Catley 1993).

The results suggest that maturity molting and sexual activity occur at the beginning of the cool period, which is also supported by the collection dates of Holmberg (1882), Gertsch & Platnick (1979) and Pérez-Miles et al. (1993). In the field Pérez-Miles et al. (1993) found adult males from May to September, with a peak of activity in July. These authors interpreted the fall/winter activity as a way to avoid predation. We also interpreted the synchronized male maturity in the same way, satiating the scarce winter predators. A capture of a male in October in Sierra de la Ventana, Argentina (Gertsch & Platnick 1979) seems to be extremely late. However, several captive males remained alive during september and a few in October, suggesting a longer lifespan in the laboratory. The male activity period of *M. thorelli* resembles a "stenochronous, winter-mature species" of Schaefer (1987), a category mainly occupied by Linyphiidae in Europe. However, this species has a longer lifespan – at least three years. Individuals molt more than expected for their size and have two periods without molting (winter and summer). The wide range of sizes found in field samples and laboratory developmental data suggest the coexistence of at least three generations.

Reproduction.—As far as we know, our observations of the sexual behavior of *M. thorelli* are the first ever published for any species of Mecicobothiidae. Females of *M. thorelli* may release a sex pheromone, which has previously been reported for Mesothelae (Haupt 1977) and several families of Mygalomorphae: Antrodiaetidae (Coyle & Icenogle 1994), Atypidae (Coyle & Shear 1981), Dipluridae (Coyle 1985, 1986b), Nemesiidae (Buchli 1962; Costa 1982) and Theraphosidae (Baerg 1958; Minch 1979; Pérez-Miles & Costa 1992). This wide distribution indicates that tactochemical sexual communication is an early aquisition in spiders. The effect of a sexual pheromone of *M. thorelli* should be of short duration and/or it would only be released

near the retreat, considering that males started the courtship in the sheet web.

Courtship characteristics suggest that vibrations transmitted through the silk threads are the primary means of communication before direct contact. Male sexual behavior strongly inhibited female attacks. The extreme passivity of females during courtship, copulation and postcopulation is remarkable, although it is common in mygalomorphs (Jackson & Pollard 1990). Only if we manipulated a couple during copulation was the male attacked and cannibalized.

Cheliceral sexual clasping has been reported in Mygalomorphae only for *Atypoides riversi* O.P.-Cambridge 1883 (Antrodiaetidae; Coyle 1971) but not involving fang clasping as in *M. thorelli*. However, it resembles that of some Araneomorphae. For example, in some species of *Pachygnatha* Sundevall 1923 and *Tetragnatha* Latreille 1804 (Tetragnathidae) males immobilize female chelicerae with their own modified chelicerae (Bristowe 1941). Also males of *Hypomma bituberculatum* (Wider 1834) (Linyphiidae) (Bristowe 1931, 1941) and *Argyrodes antipodiana* (O.P.-Cambridge 1880) (Theridiidae) (Whitehouse 1987) immobilize female chelicerae by stimulating female biting on male frontal tubercles. In Theraphosidae, precopulatory and copulatory female clasping on tibial spurs of male forelegs is a well-known mechanism (Baerg 1928, 1958; Minch 1979; Pérez-Miles & Costa 1992). The sexual embrace, behavior and reproduction of Mygalomorphae were reviewed by Coyle (1985, 1986b), Coyle & O'Shields (1990), Jackson & Pollard (1990) and Costa & Pérez-Miles (1992).

The male of *M. thorelli* elicits female clasping by pushing her with his chelicerae repeatedly. The cheliceral embrace is a *sine qua non* condition for a successful copulation. Female biting appears to cancel the aggressive and/or predatory impulse and consequently inhibit further attacks. In *Alopecosa cuneata* (Clerck 1757) (Lycosidae), where males offer their incrassate foreleg tibiae for female biting (Kronestedt 1979, 1990) a similar explanation could be applied. The release of aphrodisiac pheromones from these male structures was also suggested (Kronestedt 1986; Whitehouse 1987).

In Mecicobothriidae, cheliceral clasping is only present in *M. thorelli*. In *Megahexura*

Kaston 1972 and *Hexura* Simon 1884, males have a series of short spines above the chelicerae, distally stronger (Gertsch & Platnick 1979), suggesting their use in copulation. These structures may perform a similar to that found in *Atypoides riversi* (Antrodiaetidae). Coyle (1971) observed that in this species the males used their long cheliceral apophyses to hold the outspread female chelicerae during copulation. Clasping of *M. thorelli* might have evolved from a frontal fight with full contact of chelicerae, common in agonistic encounters. In successive steps male chelicerae would be modified to neutralize female biting and increase male security during copulation. Clasping also serves in communication and epigamic sexual selection, as well as to hold female in position (Coyle 1985, 1986b; Eberhard 1985; Jackson & Pollard 1990).

In its initial stages cheliceral clasping requires very complex movements. Positional reconstruction with dead specimens helped us understand the mechanics of clasping. We were able to verify that: 1) Both male and female must separate the basal segments of the chelicerae laterally; 2) Females must fully open the cheliceral fangs obliquely; 3) The introduction of the female fangs is initially divergent and finally convergent; 4) Female fangs enter the male cheliceral channels up to the basal incrassate region. Male hinge-like movements facilitate this rigid clasping position; 5) *In copula,* the basal chelicerae of female and male remain closed; 6) Two simultaneous procedures are necessary for unclasping: male cheliceral opening with hinge-like movements, and female cheliceral opening with fangs relaxed; 7) Males must move downward and the female upward.

Male safety during copulation is reinforced by positioning the forelegs on the female, which probably prevents the female from biting the male prosoma. The long palps of the male allow him to copulate more horizontally than other mygalomorphs. Consequently, mating can take place safely inside the retreat. Also, male backward movements probably improve clasping.

Copulation of *M. thorelli* is very complex and long in comparison with other mygalomorph spiders. The insertion/withdrawal palpal movements deserve special attention. The palpal embolus is rigid and spiral-shaped and cannot enter by rotation as in other araneo-

morphs or *Latrodectus* (Abalos & Báez 1967; Grasshoff 1973). The palpal embolus must enter forcibly, spiral by spiral, in a discontinuous jerky movement which would explain the female's sudden movements. This penetration appears to be made possible by the elasticity of the embolus, as well as the spermathecae. The number of embolus spirals and spermathecae spirals are the same – four. This close correspondence suggests that the whole embolus enters the inner spiral-shaped receptacle but not in the outer round receptacles (see fig. 38 in Gertsch & Platnick 1979). This unique penetration pattern probably causes intense genitalic stimulation which would determine sexual selection by female choice, following Eberhard's theory (Eberhard 1985). This stimulation might also have an inhibitory function on non-sexual female behaviors.

The characteristics of both embolus and receptacle spirals require that the palpal insertions must be crossed (right palp in right receptacle, and left palp in left receptacle). This crossed insertion is the norm in araneomorphs but has not been indicated yet for the mygalomorphs. Although the insertion mode is not evident from direct observation, it was confirmed from the study of helicoidal orientation complementarity between male and female genitalia. The orientation of both embolus tips and receptacle basis would also suggest that only crossed palpal insertion is possible. The wide separation between receptacle bases would facilitate a correct insertion.

Male postcopulatory behavior in *M. thorelli* is remarkable. Some males seemed to practice postcopulatory mate guarding, which would be predicted on the basis of this species spermathecal morphology (cul-de-sac type of Austad 1984). Mate guarding prevents later copulations with other males and consequently sperm competition, but can be only maintained for a brief time. Although the morphology of the receptacle stalk is adequate for mating plugs, males recopulated normally, which suggests the absence of mate plugs in *M. thorelli*.

Unlike mate guarding, female expulsion is an uncommon male postcopulatory behavior in spiders, and without a clear interpretation in *M. thorelli*. Isolated males may have an excessive aggressive motivation due to the absence of fights in natural male-male encounters. Another factor would be the fragmentary webs constructed by females in the laboratory; these would facilitate female expulsion. In the laboratory, females with deep retreats were less likely to be expelled than were those with shallow retreats; in the field deep retreats were the only type observed. However, high female tolerance to males seems to be a species-specific tactic which could be understood if combined with cryptic female location.

In the laboratory, copulated females did not spin intensely in winter and they dug deeply into the soil. Usually they did not make an exterior sheet for prey capture, and therefore would not be found by males (nor collectors). This cryptic postcopulatory female behavior, together with female expulsion by the male, could protect the paternity of the copulating male. Our hypothesis agrees with the high competition expected among males of *M. thorelli* which reach maturity synchronously and have an activity peak in July (Pérez-Miles et al. 1993).

At first, our hypothesis fails to explain the benefits from the female perspective because she loses her web and, consequently, the possibility of other copulations. New copulations would increase the variation of her offspring and avoid the risk of a single copulation with an sterile male. (See Austad 1984 for a review of remating advantages for females). However, some female benefits could be suggested.

If prey were scarce in winter, it would be more economical for a female to suspend predation and thereby avoid the cost of web maintenance, predation and parasitism risks, considering the low metabolic rates of the spider in this season. The risk to the female during expulsion from the retreat would be minimal if a low predation level in winter is assumed (Pérez-Miles et al. 1993). Webs could elicit persistent courting males which make prey capture difficult and also attract predators. This would help to explain the "complicity" of the female in allowing the weak male to expel her. Two field observations are consistent with the hypothesis: 1) we did not find adult females in September, when intense collections were carried on, and 2) a male found by Holmberg in 1881 was probably occupying a web of an expelled female.

M. thorelli make eggsacs earlier (at the end of winter and end of spring) than North American Mecicobothriidae (spring and summer) (Gertsch & Platnick 1979). The eggsacs of

these species are round as in *M. thorelli*, except in *Hexura rothi* Gertsch & Platnick 1979 (lenticular). The number of eggs is related to spider size: *M. thorelli* (body length approximately 7 mm) laid between 23–33 eggs; *Hexura rothi* (body length approximately 11 mm) laid 80 eggs, *Hexurella* Gerstch & Platnick 1979 species (body length between 3–4 mm) laid only 4–7 eggs (Gertsch & Platnick 1979).

Phylogeny and biogeography.—The monophyly of Mecicobothriidae, supported by Gertsch & Platnick (1979), Raven (1985) and Goloboff (1993), is considered as a starting point to discuss some biogeographical aspects. The amphitropical distribution of the Mecicobothriidae is similar to that reported to some coleopterans, fishes and plants (Humphries & Parenti, 1986). According to Gertsch & Platnick (1979) and Raven (1985), *Hexurella* seems to be the sister genus of the rest of Mecicobothriidae and consequently *Mecicobothrium* is more closely related to the mecicobothriid genera *Megahexura* and *Hexura* than to *Hexurella*. Considering the present geographic distribution of these taxa, only an ancient generic cladogenesis (pangeic) could be hypothesized, prior to the separation of the Americas. Avoiding dispersalist interpretations, a post-pangeic cladogenesis of North American genera could only be proposed if *Mecicobothrium* was the sister genus of the rest of Mecicobothriidae.

ACKNOWLEDGMENTS

LITERATURE CITED

Abalos, J.W. & E.C. Báez. 1967. The spider genus *Latrodectus* in Santiago del Estero, Argentina. Animal Toxins, Pergamon Press, Oxford & New York.

Austad, S.N. 1984. Evolution of sperm priority patterns in spiders. Pp. 223–249. *In* Sperm Competition and the Evolution of Animal Mating Systems. (R.L. Smith, ed.). Academic Press, San Diego, California.

Baerg, W.J. 1928. The life cycle and mating habits of the male tarantula. Quart. Rev. Biol., 3:109–116.

Baerg, W.J. 1958. The Tarantula. Univ. Kansas Press, Lawrence, Kansas.

Barrowclough, G.F. 1992. Systematics, biodiversity, and conservation biology. Pp. 121–143. *In* Systematics, Ecology, and the Biodiversity Crisis. (N. Eldredge, ed.), Columbia Univ. Press, New York.

Bristowe, W.S. 1931. The mating habits of spiders: a second supplement, with the description of a new thomisid from Krakatau. Proc. Zool. Soc. London, 27:395–413.

Bristowe, W.S. 1941. The Comity of Spiders. 2, Ray Society, London.

Buchli, H. 1962. Note préliminaire sur l'accouplement des araignées mygalomorphes *Nemesia caementaria, Nemesia dubia* et *Pachylomerus piceus* (Ctenizidae). Vie Milieu, 13:167–178.

Capocasale, R.M., F. Pérez-Miles, F.G. Costa, E. Gudynas & L. Prandi. 1989. Comunicación preliminar sobre la aracnofauna criptozoica de Sierra de las Animas, Uruguay. Bol. Soc. Zool. Uruguay, 5:31–32.

Capocasale, R.M. & E. Gudynas. 1993. La fauna de opiliones (Arachnida) del criptozoos de Sierra de las Animas (Uruguay). Aracnología, 19/20:1–15.

Catley, K.M. 1993. Courtship, mating and post-oviposition behaviour of *Hypochilus pococki* Platnick (Araneae, Hypochilidae). Mem. Queensland Mus. 33:469–474.

Costa, F.G. 1982. Etología. *In* F. Pérez-Miles & R.M. Capocasale. Hallazgo de una tercera especie del género *Pycnothelopsis*: *Pycnothelopsis tacuariensis* sp. nov. (Araneae, Pycnothelidae). Com. Zool. Mus. Hist. Nat. Montevideo, 11:1–7.

Costa, F.G. & F. Pérez-Miles. 1992. Notes on mating and reproductive success of *Ceropelma longisternalis* (Araneae, Theraphosidae) in captivity. J. Arachnol., 20:129–133.

Costa, F.G. & F. Pérez-Miles. 1994. Ecología de los escorpiones Bothriuridae de Sierra de las Animas, Maldonado, Uruguay. Aracnología, 21:1–5.

Costa, F.G., F. Pérez-Miles, E. Gudynas, L. Prandi & R.M. Capocasale. 1991. Ecología de los arácnidos criptozoicos, excepto ácaros, de Sierra de las Animas (Uruguay). Ordenes y familias. Aracnología, 13/15:1–41.

Coyle, F.A. 1971. Systematics and natural history of the mygalomorph spider genus *Antrodiaetus* and related genera (Araneae: Antrodiaetidae). Bull. Mus. comp. Zool., 141:269–402.

Coyle, F.A. 1985. Observations on the mating behavior of the tiny mygalomorph spider, *Microhexura montivaga* Crosby & Bishop (Araneae, Di-

pluridae). Bull. British Arachnol. Soc., 6:328–330.

Coyle, F.A. 1986a. The role of silk in prey capture by nonaraneomorph spiders. Pp. 269–305. *In* Spiders: Webs, Behavior, and Evolution. (W.A. Shear, ed.). Stanford Univ. Press, Stanford, California.

Coyle, F.A. 1986b. Courtship, mating, and the function of male-specific leg structures in the mygalomorph spider genus *Euagrus* (Araneae, Dipluridae). Proc. Ninth Internat. Congr. Arachnol., Pp. 33–38.

Coyle, F.A. & W.R. Icenogle. 1994. Natural history of the Californian trapdoor spider genus *Aliatypus* (Araneae, Antrodiaetidae). J. Arachnol., 22:225–255.

Coyle, F.A. & T.C. O'Shields. 1990. Courtship and mating behavior of *Thelechoris karschi* (Araneae, Dipluridae), an African funnelweb spider. J. Arachnol., 18:281–296.

Coyle, F.A. & Shear, W.A. 1981. Observations on the natural history of *Sphodros abboti* and *Sphodros rufipes* (Araneae, Atypidae), with evidence for a contact sex pheromone. J. Arachnol., 9:317–326.

Eberhard, W.E. 1985. Sexual selection and animal genitalia. Harvard Univ. Press, Harvard, Massachusetts.

Grasshoff, M. 1973. Konstruktions-und Funktionsanalyse an Kopulationsorganen einiger Radnetzspinnen. Aufs. u. Red. Senckenberg naturf. Ges., 24:129–151.

Gertsch, W.J. & N.I. Platnick. 1979. A revision of the spider family Mecicobothriidae (Araneae, Mygalomorphae). American Mus. Nov., 2687:1–32.

Goloboff, P.A. 1993. A reanalysis of mygalomorph spider families (Araneae). American Mus. Nov., 3056:1–32.

Goloboff, P.A. & Ramirez, M.J. 1991. A new species of *Drymusa* (Araneae: Scytodoidea) from Argentina. J. New York Entomol. Soc., 99:691–695.

Haupt, J. 1977. Preliminary report on the mating behaviour of the primitive spider *Heptathela kimurai* (Kishida) (Araneae, Liphistiomorphae). Z. Naturforsch., 32:312–314.

Holmberg, E.L. 1882. Observations à propos du sous-ordre des araignées territelaires (Territelariae) spécialement du genre Nord-Américain *Catadysas*, Hentz et de la nouvelle famillie Mecicobothrioidae, Holmb., Bol. Acad. Argentino, 4:153–174.

Humphries, C.J. & L.R. Parenti. 1986. Cladistic biogeography. Clarendon Press, Oxford.

Jackson, R.R. & S.D. Pollard. 1990. Intraspecific interactions and the function of courtship in mygalomorph spiders: a study of *Porrhothele antipodiana* (Araneae: Hexathelidae) and a literature review. New Zealand J. Zool., 17:499–526.

Kronestedt, T. 1979. Etologiska karaktärer vid taxonomiska studier av vargspindlar. Entomol. Tidskr., 100:194–199.

Kronestedt, T. 1986. A presumptive pheromone-emitting structure in wolf spiders (Araneae, Lycosidae). Psyche, 93:127–131.

Kronestedt, T. 1990. Separation of two species standing as *Alopecosa aculeata* (Clerck) by morphological, behavioural and ecological characters, with remarks on related species in the *pulverulenta* group (Araneae, Lycosidae). Zool. Scripta, 19:203–225.

Minch, E.W. 1979. Reproductive behaviour of the tarantula *Aphonopelma chalcodes* Chamberlin (Araneae: Theraphosidae). Bull. British Arachnol. Soc., 4:416–420.

Pérez-Miles, F. & F.G. Costa. 1992. Interacciones intra e intersexuales en *Grammostola mollicoma* (Araneae, Theraphosidae) en condiciones experimentales. Bol. Soc. Zool. Uruguay, 7:71–72.

Pérez-Miles, F., F.G. Costa & E. Gudynas. 1993. Ecología de una comunidad de Mygalomorphae criptozoicas de Sierra de las Animas, Uruguay (Arachnida, Araneae). Aracnología, 17/18:1–22.

Raven, R.J. 1985. The spider infraorder Mygalomorphae (Araneae): Cladistics and systematics. Bull. American Mus. Nat. Hist., 182:1–180.

Schaefer, M. 1987. Life cycle and diapause. Pp. 331–347, *In* Ecophysiology of spiders. (W. Nentwig, ed.). Springer Verlag, Berlin.

Whitehouse, M.E.A. 1987. The external structural detail of the protrusions on the cephalothorax of male *Argyrodes antipodiana* (Theridiidae). Bull. British Arachnol. Soc., 7:142–144.

DRAGLINE-MEDIATED MATE-SEARCHING IN
TRITE PLANICEPS (ARANEAE, SALTICIDAE)

Phillip W. Taylor[1]:   Department of Zoology, University of Canterbury, Private Bag 4800, Christchurch 1, New Zealand

ABSTRACT.   *Trite planiceps* Simon 1899, a common New Zealand jumping spider (Salticidae), lives in the cavities formed by rolled-up leaves of New Zealand flax (*Phormium tenax*) and similar plants. This study presents evidence that *T. planiceps* males use cues from females' draglines deposited on the outside of these rolled-up leaves when searching for females hidden from view inside.

In choice tests, *T. planiceps* males preferentially associated with draglines deposited by conspecific females rather than areas lacking draglines. In contrast, females did not discriminate between areas with and without males' draglines and neither males nor females discriminated between areas with and without same-sex conspecifics' draglines. Additionally, *T. planiceps* males found openings and entered the cavities within rolled-up leaves occupied by females in nature sooner when leaves were tested within 24 hours of collecting (dragline cues deposited on leaves in nature) than after the same leaves had been cleaned and aged for seven days (dragline cues removed). Shorter latency to finding of leaf openings was restored after the same leaves were subsequently occupied by females in the laboratory (dragline cues replaced). The specific cues detected by *T. planiceps* males are probably pheromones loosely bound to females' draglines.

Jumping spiders (Salticidae) differ from other spiders by having remarkably acute vision (Blest et al. 1990) and are well-known for their elaborate use of vision when hunting, navigating, and communicating (Crane 1949; Hill 1979; Clark 1994; Jackson & Pollard 1996; Li & Jackson 1996). Although salticids depend on their acute vision for many tasks, evidence from laboratory studies suggests that chemical cues associated with females' draglines are important to male salticids searching for mates. Species and sex-specific pheromones appear to be loosely bound to the draglines of female salticids, eliciting courtship or associative behavior in males of some species (Oden 1981 in Pollard et al. 1987; Jackson 1987; Clark & Jackson 1995). Additionally, males of one species, *Carrhotus xanthogramma* (Latreille 1819), have been shown to walk more slowly and recognize dummy females as prospective mates more frequently when females' draglines are present (Yoshida & Suzuki 1981).

Females of *Trite planiceps* Simon 1899, a common New Zealand salticid, build their nests in the cavities formed by rolled-up leaves of New Zealand flax (*Phormium tenax*) and similar plants (Forster & Forster 1973; Taylor 1997). Usually there is only a single small opening to these cavities (Fig. 1); males seeking females hidden from view inside rolled-up leaves face the challenge of finding these openings in a habitat containing many similar leaves that do not contain females. This study presents evidence that *T. planiceps* males use cues from draglines left by females on their 'home leaves' to identify occupied leaves and facilitate mate-searching.

METHODS

Substrate preferences.—This experiment was designed to investigate the tendencies of *T. planiceps* males and females to associate with or avoid areas containing draglines deposited by male and female conspecifics. Fifty three subadult females (penultimate molt) were collected near Christchurch, New Zealand, 2–8 weeks prior to testing and those that molted to adult were used in experiments as virgin females. Sixty eight adult males and 121 mated adult females (most females were collected from nests containing juveniles and all had distinctive white mating plugs in genital pores) were also collected from the same site 2–4 weeks prior to testing. All spiders

[1] Current address: Department of Entomology, The Hebrew University of Jerusalem, P.O. Box 12, Rehovot 76100, Israel.

Figure 1.—*Trite planiceps* male entering the cavity formed by a rolled-up leaf of New Zealand flax (*Phormium tenax*). Spider's body length = 11 mm.

Figure 2.—Diagram showing the arena used to test substrate preferences (viewed from above with the two 'half arenas' separated). (A) Opaque plastic screens. (B) 10 mm diameter hole for insertion of the transfer tube.

were maintained using standard methods (Jackson & Hallas 1986). Voucher specimens of *T. planiceps* have been deposited by Robert Jackson at the Florida State Collection of Arthropods (Gainesville).

Procedures closely resemble those used by Clark & Jackson (1994). The arena was constructed from a 90 mm-diameter plastic petri dish (Fig. 2). The petri dish (base and lid) was cut in half, and an opaque plastic screen was glued into each half-base midway between the cut edge and the point of greatest distance to the cut edge. A 10 mm-diameter half-circle hole was melted into the cut edge of each half petri dish immediately adjacent to the wall at the end to which the screen was fixed.

One 'half-arena' was selected at random to be 'draglined'. The half-circle hole and open side of this half-arena were taped over and a 'source spider' was introduced. The source spider was left for 2 h to deposit draglines. After removing the source spider, the draglined half-arena was used in a test within the following 2 h.

To begin a test, the draglined half-arena was matched up with a clean half-arena so that the half-circle holes on the edge of the half-arenas

formed a single 10 mm-diameter hole in the floor. The 'test spider' was placed in a clear plastic 'transfer tube' (40 mm × 10 mm external diameter) which was then corked at both ends. The transfer tube was inserted into the hole in the arena floor so that the tube protruded 1–2 mm into the arena and was held in place by the two half-arenas pressing together. The cork protruding into the arena was then removed and the two half lids were slid into place. The test spider climbed up out of the transfer tube into the arena, and the test began when the spider's palps were above the arena surface. The amount of time that the test spider spent on each side of the arena was recorded for 10 min, using the palps as the point of reference for location. If a spider stood with one palp on each side of the arena, it was counted as still being on the side previously occupied by both palps (i.e., failing to move to the other side). Each spider was used only once as a test spider or source spider for any particular treatment (e.g., male on male draglines).

Mate-searching on rolled-up leaves.— This experiment was designed to investigate whether mate-searching by *T. planiceps* males is facilitated by draglines left by conspecific females on leaf surfaces in the laboratory, and whether similar cues are present in nature.

Fresh leaf tests: Twenty rolled-up flax

Figure 3.—Diagram showing the arena used to test the effects of dragline cues on mate-searching efficiency. (A) Arrows indicating two dried leaves that are not rolled-up. (B) Rolled-up leaf. (C) Arrow indicating the opening of the cavity within the rolled-up leaf. The same spatial arrangement of leaves was adopted for all tests.

leaves containing *T. planiceps* nests and maternal females were collected on the evening prior to testing. Fresh leaves would typic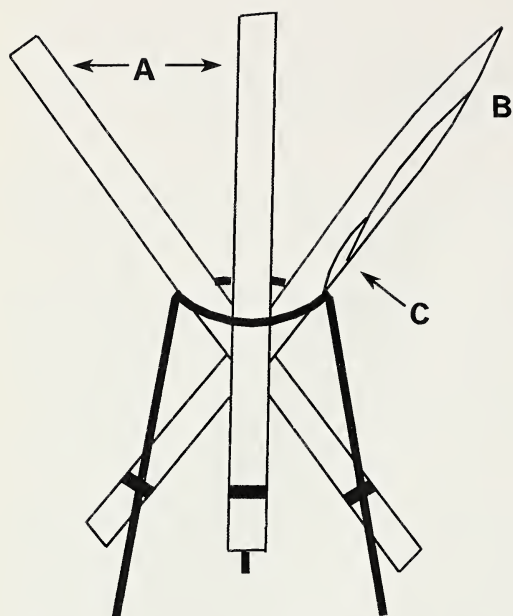ally be covered by draglines deposited by resident females in nature. Because many salticid pheromones are water-soluble (Jackson 1987), and therefore susceptible to being depleted by rain, leaves were collected at least 5 days after the most recent rainfall. Residents were removed, and the rolled-up leaves were cut to 500–550 mm long with the opening near the middle.

On the day of testing, each rolled-up leaf was mounted (using plastic insulating tape) on a tripod with two other dried leaves (500–550 mm long) that were not rolled up (Fig. 3). The tripod and attached leaves were placed in a clean glass tank (300 mm × 300 mm floor, 600 mm high). The opened cage of a *T. planiceps* male was placed on the tank floor and the tank was sealed with a glass lid. All experiments were started in the middle 2 h of the laboratory light phase (12L:12D). After the male left his cage I recorded, at 5 min intervals for a maximum period of 5 h, wheth-

er the male had entered the cavity within the rolled-up leaf. If the male could not be seen in the tank, the rolled-up leaf was carefully unrolled to confirm that the male was inside (end of test). Each leaf was used only once (i.e., 20 tests in total).

Cleaned leaf tests: After fresh leaf tests ended, the glass tanks, tripods and leaves (each of the 20 tripod and leaf setups were kept intact) were thoroughly washed with distilled water and then ethanol to remove draglines and pheromones. They were then left for 7 days, so that remaining pheromones could dissipate, and the testing procedure was repeated. This treatment's title 'cleaned leaves' was justified because, in other salticids, aging and washing with polar solvents such as water is known to eliminate the effectiveness of draglines at eliciting associative behavior and courtship of males (Jackson 1987; Clark & Jackson 1995).

Lab-draglined leaf tests: After cleaned leaf tests the 20 tanks, tripods and leaves (tripod and leaf setups still intact) were washed again and allowed to dry for 24 h. The adult female that was in the leaf in nature was then replaced in the leaf, left for 7 days in the closed tank, and testing was repeated again. On the day before testing a lab-draglined leaf, the resident was removed and the whole arena (tank, tripod, leaves), except the rolled-up leaf, was washed.

The same group of 20 males was used for the 20 tests using fresh, cleaned, and lab-draglined leaves, but each male was used only once per treatment and the same male was not used for more than one treatment of a particular leaf. To ensure that results were not confounded by shrinkage of the openings of rolled-up leaves during the interval between treatments, maximum width and length of openings were measured to the nearest millimeter following the first and third treatments, and compared.

RESULTS

Substrate preferences.—Males spent more time on the side of the arena containing draglines of conspecific females than on the clean side but there was no evidence that females (mated or virgin) either associated with or avoided draglines deposited by males (Table 1). Also, neither males nor females showed

Table 1.—Proportions of total time spent on the draglined half-arena *vs.* clean half-arena. Comparisons are by Wilcoxon signed ranks test.

Test spider	Source spider	n	median	Upper quartile	Lower quartile	P
Male	Mated female	47	0.78	0.91	0.52	<0.001
Mated female	Male	37	0.48	0.77	0.30	>0.3
Virgin female	Male	37	0.47	0.63	0.34	>0.5
Male	Male	56	0.51	0.68	0.34	>0.4
Mated female	Mated female	92	0.56	0.69	0.36	>0.5

any tendency to associate with or avoid draglines of same-sex conspecifics (Table 1).

Mate-searching on rolled-up leaves.— Males found the openings and entered the cavities within rolled-up leaves during the 5 h testing period in all tests using fresh ($n = 20$) or lab-draglined leaves ($n = 20$), and in 18 of 20 tests using cleaned leaves (Fisher exact test, $P > 0.3$). However, latency until entering cleaned rolled-up leaves (median 83 min; quartiles 33–136 min) was greater than for fresh leaves (median 23 min; quartiles 12–42 min; Wilcoxon signed ranks test, $P < 0.005$) or lab-draglined leaves (median 18 min; quartiles 11–25 min; Wilcoxon signed ranks test, $P < 0.001$). There was no evidence that latency to entry of rolled-up leaves differed for fresh and lab-draglined leaves (Wilcoxon signed ranks test, $P > 0.2$). Also, there was no evidence that length or width of the openings to rolled-up leaves changed during the three week interval between tests (Wilcoxon signed ranks test, for both dimensions $P > 0.9$).

DISCUSSION

Males of some salticids begin courting when they come into contact with draglines deposited by conspecific females (Jackson 1987). Although females' draglines do not elicit courtship in *T. planiceps* males (Jackson 1987), the present study shows that females' draglines do elicit associative behavior in males of this species. In this respect, *T. planiceps* resembles *Portia fimbriata* (Doleschall 1859) and *P. labiata* (Thorell 1882), the only other salticids for which comparable data are available (Jackson 1987; Clark & Jackson 1995). Although other possibilities cannot be ruled out, related studies suggest the specific relevant cues eliciting association in *T. planiceps* males are pheromones loosely bound to

the nest and dragline silk of females (Jackson 1987, Oden 1981 in Pollard et al. 1987, Clark & Jackson 1994).

In addition to associating with females' draglines in choice tests, *T. planiceps* males found females' nesting sites sooner when females' draglines were present on rolled-up leaves. Although increased success at mate-searching may be explained by associative behavior alone, we should also consider the possibility that *T. planiceps* males actively searched for the openings of rolled-up leaves when they contacted the draglines. Female salticids typically build their nests in only a narrow range of easily identified microhabitats (Hallas & Jackson 1986) and commonly reside at a single nesting site with their developing young for many weeks (Jackson 1979; Taylor 1997). Brooding females deposit draglines as they move about near their nests, and this would be the most common natural context in which an area would be densely covered by draglines. Male salticids that encounter dragline-covered areas might next search visually both for females directly and for typical nesting microhabitats.

The present study of *T. planiceps* has an important feature that emulates nature more completely than previous studies using other salticids. In addition to using draglines deposited in the laboratory (all tests of association and 'lab-draglined leaves'), I also used leaves on which draglines had been deposited in nature ('fresh leaves'). Identifying a similar response to lab-draglined and fresh leaves strengthens the assertion that dragline cues are present and used by *T. planiceps* males searching for mates in nature. The need for such confirmation was highlighted by Persons & Uetz (1996) in the context of predation. These authors found that a lycosid spider,

Schizocosa ocreata (Hentz 1844), associates with areas recently occupied by large numbers of crickets but express doubt that adequate concentrations of the kairomones responsible would occur naturally. Similar doubts could be expressed about studies of how salticids use dragline-cues, as none have confirmed that similar cues are present in adequate density in nature. Results of this study provide some assurance that laboratory assays of salticid responses to dragline-cues produce results that are indeed relevant in nature.

ACKNOWLEDGMENTS

LITERATURE CITED

Blest, A.D., D.C. O'Carroll & M. Carter. 1990. Comparative ultrastructure of layer I receptor mosaics in principal eyes of jumping spiders: the evolution of regular arrays of light guides. Cell Tiss. Res., 262:445–460.

Clark, D.L. 1994. Sequence analysis of courtship behavior in the dimorphic jumping spider *Maevia inclemens* (Araneae, Salticidae). J. Arachnol., 22:94–107.

Clark, R.J. & R.R. Jackson. 1994. Self recognition in a jumping spider: *Portia labiata* females discriminate between their own draglines and those of conspecifics. Ethol. Ecol. Evol., 6: 371–375.

Clark, R.J. & R.R. Jackson. 1995. Dragline-mediated sex recognition in two species of jumping spiders (Araneae, Salticidae), *Portia labiata* and *P. fimbriata*. Ethol. Ecol. Evol., 7:73–77.

Crane, J. 1949. Comparative biology of salticid spiders at Rancho Grande, Venezuela. Part IV. An analysis of display. Zoologica, 34:159–214.

Forster, R.R. & L.M. Forster. 1973. New Zealand spiders. Collins, Auckland.

Hallas, S.E.A. & R.R. Jackson. 1986. Prey-holding abilities of the nests and webs of jumping spiders (Araneae, Salticidae). J. Nat. Hist., 20:881–894.

Hill, D.E. 1979. Orientation by jumping spiders of the genus *Phidippus* (Araneae, Salticidae) during the pursuit of prey. Behav. Ecol. Sociobiol., 5: 301–322.

Jackson, R.R. 1979. Nests of *Phidippus johnsoni* (Araneae, Salticidae): Characteristics, pattern of occupation, and function. J. Arachnol., 6:1–29.

Jackson, R.R. 1987. Comparative study of releaser pheromones associated with the silk of jumping spiders (Araneae, Salticidae). New Zealand J. Zool., 14:1–10.

Jackson, R.R. & S.E.A. Hallas. 1986. Comparative biology of *Portia africana, P. albimana, P. fimbriata, P. labiata,* and *P. shultzi,* araneophagic, web-building jumping spiders (Araneae: Salticidae): utilization of webs, predatory versatility, and intraspecific interactions. New Zealand J. Zool., 13:423–489.

Jackson, R.R.& S.D. Pollard. 1996. Predatory behavior of jumping spiders. Annu. Rev. Entomol., 41:287–308.

Li, D. & R.R. Jackson. 1996. Prey preferences of *Portia fimbriata*, an araneophagic, web-building jumping spider (Araneae: Salticidae) from Queensland. J. Insect Behav., 9:613–642.

Persons, M.H. & G.W. Uetz. 1996. Wolf spiders vary patch residence time in the presence of chemical cues from prey (Araneae, Lycosidae). J. Arachnol., 24:76–79.

Pollard, S.D., A.M. MacNab & R.R. Jackson. 1987. Communication with chemicals: pheromones and spiders. Pp. 133–141. *In* Ecophysiology of spiders. (E. Nentwig, ed.). Springer-Verlag, Berlin.

Taylor, P.W. 1997. Brood-defense as a function of maternal brood-attendance in *Trite planiceps* (Araneae, Salticidae). Bull. British Arachnol. Soc., 10:341–343.

Yoshida, H. & Y. Suzuki. 1981. Silk as a cue for mate location in the jumping spider, *Carrhotus xanthogramma* (L.) (Araneae, Salticidae). Appl. Entomol. Zool., 16:315–317.

THE EFFECT OF CONSPECIFICS ON THE TIMING
OF ORB CONSTRUCTION IN A COLONIAL SPIDER

Elizabeth M. Jakob[1]:   Biological Sciences, Bowling Green State University, Bowling Green, Ohio 43403 USA

George W. Uetz: Biological Sciences, 821A Rieveschl, University of Cincinnati, Cincinnati, Ohio 45221-0006 USA

Adam H. Porter[1]:   Biological Sciences, Bowling Green State University, Bowling Green, Ohio 43403 USA

ABSTRACT. *Metepeira incrassata* (F.O. Pickard-Cambridge 1903) (Araneae, Araneidae) are colonial spiders that share a common and relatively permanent framework of silk, but that construct and defend individual orbs within the communal framework. Orbs are taken down nightly and replaced in the morning. Larger spiders generally begin orb construction before smaller spiders do. We tested whether this pattern results from interactions among spiders of different size classes. We constructed artificial colonies that contained either a mixture of size classes or a single size class. In two replicates, spiders that were housed in single-size groups built their orbs at the same time as their counterparts in mixed groups. We suggest that conspecific interaction is unlikely to be the only factor determining the differences in the timing of orb construction among size classes in this species.

Metepeira incrassata are colonial spiders that live in large groups and share a common space web that is relatively permanent. Within this silk framework each spider constructs its own orb and defends it against intruders. Orbs are ingested by the owners at the end of the foraging day, and rebuilt again in the morning. Within a colony, spiders are typically segregated by size: larger spiders are generally found in the core, where predation risk and food level are low, and smaller ones are generally on the periphery, where predation risk and food level are higher (Rayor & Uetz 1990; Rayor & Uetz 1993). This colony structure may occur because the optimal location within a colony differs across size classes (Rayor & Uetz 1993), or because some spiders are excluded from favorable positions by conspecifics, or a combination of both. *M. incrassata* often fight over potential orb sites, and large spiders are likely to have the advantage: size has been shown to be a determinant of winning aggressive interactions in this species (Hodge & Uetz 1990, 1995), as in other

spider species (e.g., Austad 1983; Buskirk 1975; Christenson & Goist 1979; Jakob 1991; Jakob 1994; Riechert 1978a; Riechert 1978b; Wells 1988). Large *M. incrassata* released into a colony of smaller individuals displaced smaller individuals from the core (Rayor & Uetz 1990).

Large spiders have a further advantage in web establishment because they build their orb webs earlier in the foraging period than do smaller spiders. Large spiders, followed by medium and small spiders, generally begin orb construction at first light. It is not clear if this temporal pattern in web construction occurs because of interactions between the size classes: small spiders may be inhibited by the presence of larger spiders and delay web construction, or perhaps large spiders begin web construction earlier when in the presence of smaller spiders in order to secure the best foraging sites. We tested this hypothesis by constructing small colonies with and without larger competitors, and noting the time that web building began and ended. We predicted that, if spiders are influenced by the presence of conspecifics, those in groups composed only of individuals of the same size would differ in the time of orb construction compared to spiders in mixed-size groups.

[1]Current address: Dept. of Entomology, 102B Fernald Hall, University of Massachusetts, Amherst, Massachusetts 01003-2410 USA

METHODS

The study site was in Fortin de las Flores (19°N, 97°W, 1000 m elevation), in Veracruz, Mexico (for detailed description of study area, see Uetz & Hodge 1990). Six 1 m³ cages were constructed of polyvinyl chloride ("PVC") pipe and covered with fine mesh. They were set on a patio that was open to the air but roofed so it was protected from rain. Pairs of cages were placed next to one another. The position of the cage pairs on the patio was decided randomly.

All spiders were collected from a nearby large colony, estimated to be several thousand individuals in size. In order to eliminate the need for experimental spiders to invest an unusually large amount of energy on the construction of communal space webs in the experimental cages, approximately 25 adults were introduced into each cage. After two days, these spiders were removed early in the morning prior to orb-web construction and were not used in the experiment.

For each of two replicates, we established three cages that each contained spiders of a single size class: either 15 large females (7–10 mm), 20 medium (4–6 mm), or 40 small (1–3 mm) spiders (medium and small spiders could not be sexed). Each cage of single-sized individuals was paired with a cage of mixed-size individuals that contained 15 large, 20 medium, and 40 small spiders. These numbers were chosen to reflect the typical composition of age classes and spider densities in the field. Spiders were released unmarked into the cages two days before the day of the test in order to be given time to acclimate. The two replicates were conducted five days apart.

We began watching spiders when they began to move during the hour prior to dawn. We recorded the behavior of each spider using the technique of scan sampling (Altmann 1974), in which behaviors of individuals in a group are noted in sequence. We examined each cage every 15 minutes in the same order each time. Pairs of cages were examined either simultaneously or in rapid sequence. Data collection stopped when all or nearly all webs were complete, generally around noon. For each spider, we noted on audiocassette its size, and whether it was laying down communal space web, the radii of its orb, a temporary spiral, a permanent spiral, or was sitting at the hub of a complete web (for a more detailed description of orb construction, see Foelix 1996; Uetz et al. 1994).

Because of the brevity of some of the stages in web-building relative to the 15 min interval between scans, we focused on two pieces of data: the time when permanent spirals were begun and when orbs were completed. Both measures together allowed us to examine the possibility that the presence of conspecifics does not affect the time of web initiation, but slows the process of web construction, perhaps through interruptions. We used an ANOVA design to examine simultaneously the three main effects: replicate, spider size class, and cage composition, as well as the interaction between size class and cage composition. A significant interaction would indicate that changes in the timing of web construction are influenced by group composition. The data did not fit the assumptions of standard ANOVA methods, so we used a nonparametric bootstrap analysis to obtain the null distributions of the Fs, from which we calculated the significance levels in the ANOVA design. In parametric statistical approaches, the null distributions are obtained mathematically from sampling theory, under the assumptions of normally distributed residuals and homoscedasticity of variances, and reflect the variation that would be produced in the statistics under random sampling error alone. In a bootstrap analysis, the null distributions are obtained by repeatedly calculating the statistics of interest on random samples from the original data (Efron 1982; Efron & Tibshirani 1993). This creates distributions that vary only because of sampling error, without invoking the assumptions of standard mathematical approaches. Significance may then be assessed from these null distributions by the percentile method: observed values in the nth percentile reflect significance at the $P \leq 1/(2n)$ level (Efron 1982; Efron & Tibshirani 1993). Our calculations were made using a general linear model program for ANOVA written in THINK® Pascal v4.2 (Symantec Corp.) by AHP and run on a Macintosh PowerPC® 9500, and the calculation of the ANOVA table was checked using the statistical program SuperANOVA® v1.1 (Abacus). We used 1000 bootstrap replicates in our tests; so to be conservative, we report P values to only two decimal places.
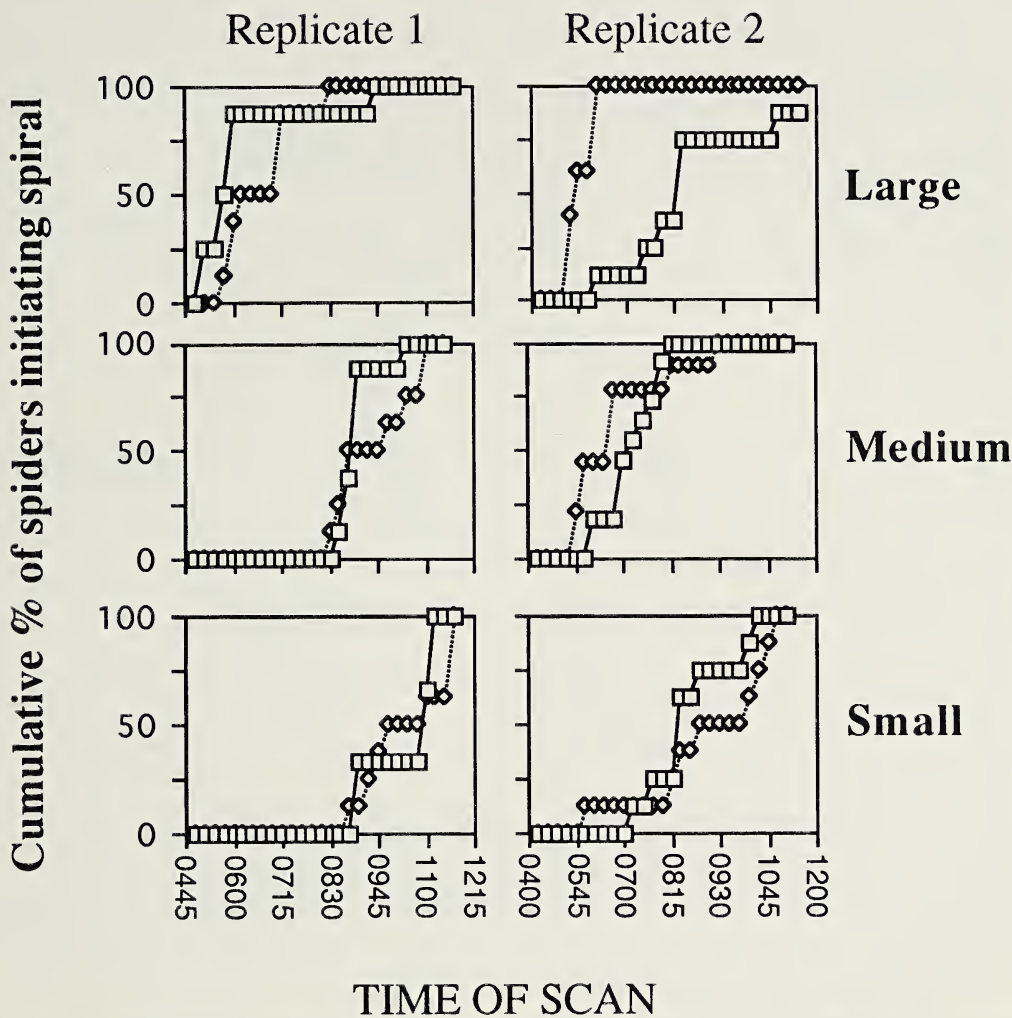
Figure 1.—Cumulative percentage of spiders that initiated the permanent spiral. Diamonds (◊) represent single-size class colonies and squares (□) represent mixed size-class colonies. The x-axis represents the starting times of scans taken at 15 minute intervals beginning at the onset of web-building activity.

Follow-up comparisons were done using Mann-Whitney U-tests for each trial.

Voucher specimens are deposited at the Museum of Comparative Zoology at Harvard.

RESULTS

Not all spiders built orbs in our experimental conditions, especially small spiders. Several molted during the course of the experiment, and spiders generally stop feeding just prior to a molt (Foelix 1996). There were no differences between the number of spiders that built webs in the different treatment types (contingency table, G-test, $P > 0.4$ in all cases; number of spiders that were active ranged from 60–92% of spiders per cage).

There were highly significant differences between replicates in the timing of web-building (Tables 1 and 2, $P < 0.01$), which probably reflect daily variation in temperature and light level (mainly cloud cover) in the early morning hours.

We confirmed previous observations that large spiders build their webs earlier than did medium spiders, which in turn build their webs before small spiders (Figs. 1–3). This is reflected in the size-class main effects of Table 1 (initiation of permanent spiral, $P < 0.01$) and Table 2 (web completion, $P < 0.01$), where small, medium and large spiders are compared. In follow-up tests, all pair-wise comparisons between size classes were signif-
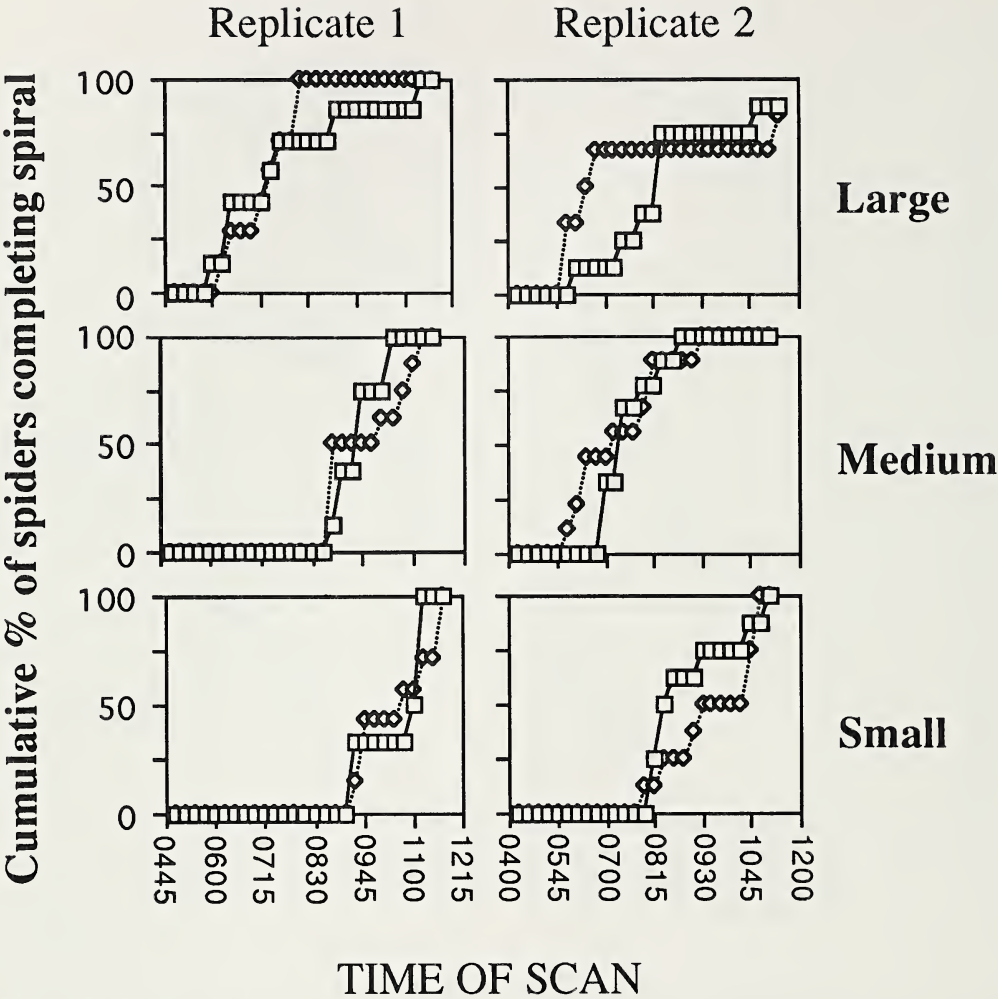
Figure 2.—Percentage of spiders with completed orbs. Diamonds (◊) indicate single-size class colonies and squares (☐) indicate mixed size-class colonies. The x-axis represents the starting times of scans taken at 15 minute intervals beginning at the onset of web-building activity.

Table 1.—ANOVA on the time of initiation of the permanent spiral. P-values are derived from 1000 bootstrap replicates.

Source	df	Sum of squares	Mean squares	F	P
replicate	1	1130.301	1130.301	41.210	<0.01
size class	2	1733.343	866.671	31.598	<0.01
cage composition	1	55.811	55.811	2.035	0.15
size class × cage composition	2	76.216	38.108	1.389	0.23
residual	85	2331.388	27.428		
Total	91	5035.163			

Table 2.—ANOVA on the time of completion of the orb. *P*-values are derived from 1000 bootstrap replicates.

Source	df	Sum of squares	Mean squares	F	P
replicate	1	477.709	477.709	17.622	<0.01
size class	2	1281.573	640.787	23.638	<0.01
cage composition	1	10.489	10.489	0.387	0.55
size class × cage composition	2	75.359	37.680	1.390	0.26
residual	85	2222.860	27.108		
Total	91	3939.978			

icant in both replicates (Mann-Whitney *U*, *P* < 0.02 in all cases) with the exception of large vs. medium spiders in replicate 2, where the timing of spiral initiation and web completion did not significantly differ. There was no discernible effect of cage composition (single-size groups vs. mixed-size groups) on the timing of web building (Figs. 1, 2; Table 1, initiation of permanent spiral, *P* = 0.15; Table 2, web completion, *P* = 0.55).

We found no evidence that interactions among spiders of different age classes were responsible for the differences in the timing of web construction. This is seen by the absence of significant interactions between spider size class and cage composition in Table 1 (initiation of permanent spiral, *P* = 0.23) and Table 2 (web completion, *P* = 0.26).
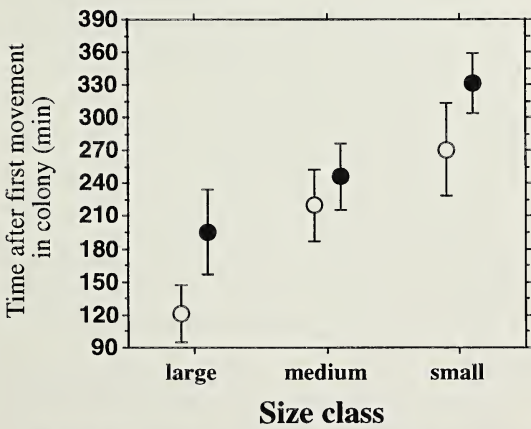

Figure 3.—Means and 95% confidence intervals of the times from when spiders in the colony first began moving to initiation of permanent spirals (○) and completed orbs (●) of the three size classes of spiders (large = 7–10 mm; medium = 4–6 mm; small = 1–3 mm).

DISCUSSION

Smaller spiders began and finished their webs later in the day than did larger spiders. We did not observe orb take-down at the end of the foraging period in this experiment, but in other colonies spiders of all sizes take down their orbs almost simultaneously (Uetz & Jakob pers. obs.), suggesting that the foraging day for smaller spiders is shorter than for larger spiders. The observation that smaller spiders built their webs later in the morning than did larger ones cannot be wholly accounted for by interactions among different size classes of spiders. We found no evidence that large spiders begin the construction of the permanent spiral earlier when medium and small spiders are present in the colony or that smaller spiders delay web construction when in the presence of larger spiders (Table 1).

What may cause the pattern of later orb construction in smaller spiders? Three explanations are possible. First, the effect of past competitive interactions cannot be excluded. We did not use naive spiders, but spiders that had been recently collected from a large colony. Individuals may have learned to avoid interactions with larger spiders and to remain quiescent while larger spiders are active in the colony. Second, even if learning is not involved, aggression between conspecifics may have led to different orb-building strategies for different size classes of spiders over evolutionary time. Third, spiders of different sizes may have different physiological constraints. Temperature, for example, affects spider development, reproduction and other life-history traits (Li & Jackson 1996). A number of species have been shown to prefer particular temperatures (reviewed in Humphreys 1987); for example, *Achaearanea tepidariorum* (C.L.

Koch) placed in a thermal gradient moved to the temperature optimal for web construction (Barghusen et al. 1997). It is possible that warmer temperatures are necessary to trigger orb-building behavior in smaller *M. incrassata* spiders. Spiders of all sizes begin building earlier in the day in warmer weather, and often pause during orb construction when clouds appear (Jakob pers. obs.). A third replicate of this experiment in which direct sunlight hit some cages earlier than others had to be discarded because spiders in the sun built significantly earlier. However, in two lycosid species, juveniles selected lower temperatures than did adults (Sevacherian & Lowrie 1972), which does not support this interpretation of *M. incrassata* behavior. Experiments under controlled temperatures are necessary to test this hypothesis.

These results differ from those in a similar experiment (L. Rayor pers. comm.) in which medium and small spiders together in colonies built an hour earlier than did those in colonies that included large spiders. Her evidence suggests that large spiders interrupt smaller spiders during orb construction. Experimental design may account for the differences in our results. Rayor allowed spiders to acclimate to the experimental colony for several days before data collection. This may have allowed smaller spiders in colonies without large spiders time to learn that they were not likely to be interrupted. In our experiment, colonies were observed two days after establishment, so spiders were not afforded the same opportunity to learn. In addition, Rayor's colonies were larger and not enclosed in cages, and perhaps this had some effect.

ACKNOWLEDGMENTS

LITERATURE CITED

Altmann, J. 1974. Observational study of behavior: sampling methods. Behaviour, 49:227–267.

Austad, S.N. 1983. A game theoretical interpretation of male combat in the bowl and doily spider *(Frontinella pyramitela)*. Anim. Behav., 31:59–73.

Barghusen, L.E., D.L. Claussen, M.S. Anderson & A.J. Bailer. 1997. The effects of temperature on the web-building behaviour of the common house spider, *Achaeranea tepidariorum*. Funct. Ecol., 11:4–10.

Buskirk, R.E. 1975. Aggressive display and orb defence in a colonial spider, *Metabus gravidus*. Anim. Behav., 23:560–567.

Christenson, T.E. & K.C. Goist, Jr. 1979. Costs and benefits of male-male competition in the orb weaving spider, *Nephila clavipes*. Behav. Ecol. Sociobiol., 5:87–92.

Efron, B. 1982. The Jackknife, the Bootstrap, and Other Resampling Plans. Vol. 38, CBMS-NSF Regional Conference Series in Applied Mathematics. SIAM.

Efron, B. & R.J. Tibshirani. 1993. An Introduction to the Bootstrap. Chapman & Hall, New York.

Foelix, R.F. 1996. The Biology of Spiders. 2nd ed. Oxford Univ. Press, Oxford.

Hodge, M.A. & G.W. Uetz. 1990. Influence of habitat and prey availability on spatial organization and behavior of colonial web-building spiders. Nat. Geogr. Res., 6:22–40.

Hodge, M.A. & G.W. Uetz. 1995. A comparison of agonistic behaviour of colonial web-building spiders from desert and tropical habitats. Anim. Behav., 50:963–972.

Humphreys, W.F. 1987. Behavioural temperature regulation. Pp. 56–65. *In* Ecophysiology of Spiders. (W. Nentwig, ed.). Springer-Verlag, Berlin.

Jakob, E.M. 1991. Costs and benefits of group living for pholcid spiders: losing food, saving silk. Anim. Behav., 41:711–722.

Jakob, E.M. 1994. Contests over prey by group-living pholcids. J. Arachnol., 22:39–45.

Li, D. & R.R. Jackson. 1996. How temperature affects development and reproduction in spiders: a review. J. Therm. Biol., 21:245–274.

Rayor, L.S. & G.W. Uetz. 1990. Trade-offs in foraging success and predation risk with spatial position in colonial spiders. Behav. Ecol. Sociobiol., 27:77–85.

Rayor, L.S. & G.W. Uetz. 1993. Ontogenetic shifts within the selfish herd: predation risk and foraging trade-offs change with age in colonial web-building spiders. Oecologia, 95:1–8.

Riechert, S.E. 1978a. Energy-based territoriality in populations of the desert spider *Agelenopsis aperta* (Gertsch). Symp. Zool. Soc. London, 42:211–222.

Riechert, S.E. 1978b. Games spiders play: behav-

ioral variability in territorial disputes. Behav. Ecol. Sociobiol., 3:135–162.

Sevacherian, V. & D.C. Lowrie. 1972. Preferred temperatures of two species of lycosid spiders, *Pardosa sierra* and *P. ramulosa*. Ann. Entomol. Soc. America, 65:111–114.

Uetz, G.W., C.S. Hieber, E.M. Jakob, R.S. Wilcox, D. Kroeger, A. McCrate & A.M. Mostrom. 1994. Behavior of colonial orb-weaving spiders during a solar eclipse. Ethology, 96:24–32.

Uetz, G.W. & M.A. Hodge. 1990. Influence of habitat and prey availability on spatial organization and behavior of colonial web-building spiders. Nat. Geogr. Res., 6:22–40.

Wells, M.S. 1988. Effects of body size and resource value on fighting behaviour in a jumping spider. Anim. Behav., 36:321–326.

COURTSHIP, COPULATION, AND SPERM TRANSFER IN *LEUCAUGE MARIANA* (ARANEAE, TETRAGNATHIDAE) WITH IMPLICATIONS FOR HIGHER CLASSIFICATION

William G. Eberhard: Smithsonian Tropical Research Institute, and Escuela de Biología, Universidad de Costa Rica, Ciudad Universitaria, Costa Rica

Bernhard A. Huber[1]:   Escuela de Biología, Universidad de Costa Rica, Ciudad Universitaria, Costa Rica

ABSTRACT.   The courtship behavior of male *Leucauge mariana* (Keyserling 1881) spiders that occurred both prior to and during copulation is described, along with the positions and movements of the male genitalia. The great variation in male behavior suggests that it does not function in species recognition. Several kinds of female response are necessary if a male is to successfully inseminate her. Males made two types of insertion, involving different movements of palpal sclerites, and copulations with virgin females differed quantitatively and qualitatively from those with non-virgins. Males deposited encapsulated sperm and other material in an outer chamber of the female's spermatheca early in copulation. Later stages of copulation involved deposition of material on the surface of the female's epigynum that sometimes resulted, with the apparent addition of material by the female, in the formation of a plug on the epigynum. Sperm were decapsulated in the female soon after insemination, perhaps as a result of the action of a female glandular product, and later were found in two other chambers of her spermathecae. Contrary to previous discussions, male and female cheliceral clasping behavior accompanying copulation does not explain why the palpal morphology of these spiders is relatively simple. Cheliceral clasping was similar, though not identical, to that of several other tetragnathine spiders. Cheliceral clasping and details of how male palps engage the female may provide synapomorphies linking *Leucauge* to tetragnathines.

RESUMEN.   Se describe el comportamiento de cortejo de machos de *Leucauge mariana* (Keyserling 1881) que ocurrió antes y durante la cópula, y las posiciones y los movimientos de la genitalia del macho. La gran variación en el comportamiento de los machos sugiere que ésto no funciona como señal de reconocimiento de la especie del macho. Varias respuestas de las hembras son necesarias par que un macho logre inseminarla exitosamente. Los machos efectuan dos tipos de inserción de los palps en los cuales realizaron diferentes movimientos con los escleritos del palpo. Las cópulas con hembras vírgenes difierieron tanto cuántitativamente como cuálitativamente de las cópulas con hembras no vírgenes. Los machos introdujeron espermatozoides encapsulados y otras sustancias en una cámara de la espermateca de la hembra durante una etapa temprana en la cópula. Después depositaron materiales sobre la superficie del epígeno que a véces formaron, en combinación con material proveniente de la hembra, un tapón sobre el epígeno. Los espermatozoides salieron de las cápsulas dentro de la hembra, quizás como resultado de la acción de un producto glandular de la hembra, y después llegaron a dos otras cámeras de la espermateca. Al contrario de algunas discusiones previas, el agarre entre los quelíceros del macho y la hembra no explica porqué la morfología de los pedipalpos del macho de este grupo es relativamente sencilla. El agarre entre quelíceros se asemeja al agarre de varias otras especies de Tetragnathinae, y este comportamiento, mas otros detalles de como los palpos del macho se acoplan con la genitalia de la hembra, pueden proveer sinapomorfías que ligan *Leucauge* a Tetragnathinae.

Male courtship behavior is often thought to function to induce the female to allow the

[1] Current address: Dept. of Entomology, American Museum of Natural History, Central Park West at 79th St., New York, New York 10024 USA.

male to initiate copulation. If this is true, then male courtship behavior that occurs after copulation has begun ("copulatory courtship") is seemingly functionless and thus paradoxical. It appears, nevertheless, that copulatory courtship is widespread in insects and spiders

(Eberhard 1991, 1994; Huber in press). It seems likely that copulatory courtship serves to induce other post-intromission female responses that are also critical to male reproductive success, such as allowing the copulation to go to completion, sperm transport (Bukowski & Christenson 1997), dumping the sperm of previous males, storing and maintaining the sperm of the current male, oviposition, and refusing the sexual advances of other males (see Eberhard 1996 for a list of 20 possible female responses).

There is a sizeable, though somewhat scattered, literature on spider mating behavior (reviewed by Robinson 1982; Jackson & Macnab 1991; Richman & Jackson 1992; and Huber in press; for more recent work on araneoids Lubin 1986; Gonzalez 1989; Gonzalez & Armendano 1995; Castro 1995; Bukowski & Christenson 1997). Although there are descriptions of male courtship during copulation (e.g., Jackson & Whitehouse 1989 on the salticid *Thorellia ensifera* [= *Thorelliola ensifera* (Thorell 1877)], in which male tapping appears to induce the female to remain quiet; see also Stratton et al. 1996; and Huber in press summarizing the extensive observations by U. Gerhardt), the emphasis has generally been on pre-copulatory courtship. There are several reasons, however, to suspect that reports have been biased against descriptions of courtship behavior after copulation has begun (Eberhard 1994).

The sexual biology of spiders in the large (> 100 species) genus *Leucauge* White 1841 has been little studied. Both newly molted virgin females and older females mate in the field (Eberhard et al. 1993). Males in the field tend to associate with immature females about to molt to maturity rather than with mature females, suggesting that sperm from a female's first mating are more likely to fertilize her eggs (Eberhard et al. 1993). Castro (1995) described several aspects of the pre-copulatory courtship in *L. venusta* (Walckenaer 1841), *L. "mandibulata"* (the specimens were of *mariana* - H.W. Levi pers. comm.) and the closely related *Plesiometa argyra* (Walckenaer 1841). Brief descriptions of copulatory courtship behavior in *L. mariana* and three other, unidentified species of *Leucauge* were given by Eberhard (1994). Female *L. mariana* build egg sacs on the ground, and cover them with particles of soil and debris (Ibarra et al. 1991). Here we use the very abundant *L. mar-*

iana (Keyserling 1881) to determine the possible significance of male copulation behavior that may be linked to events inside the female during copulation. We also describe the morphological mesh between male and female genitalia, movements of the male genitalia, the process of sperm transfer, and the phylogenetic implications of some aspects of *Leucauge* sexual behavior.

METHODS

Spiders were observed both in the field and in captivity during September and October 1989 and November 1995 near San Antonio de Escazu, and February–November 1995 in San Pedro de Montes de Oca (both in San José Province), Costa Rica. More than 40 pairs were observed courting and mating in captivity using a 8×, 20×, 40×, and 80× dissecting microscope; verbal accounts of some copulations were taped. Ten copulations were videotaped in captivity at 30 frames per second using a National Newvicon VHS camera equipped with +6 closeup lenses. One mating sequence was videotaped in the field. All drawings depicting the behavior of entire animals were traced from video images. Portions of the spiders that were not resolved in the videos were not drawn. Females whose mating history was known were obtained by collecting penultimate juvenile females that were accompanied by adult males, allowing the females to molt to maturity in captivity (in all cases this occurred within three days or less), and then mating them one to seven days later.

The silk lines on which the spiders met varied, and seemed to have no effect on subsequent courtship and mating. The female was allowed to spin a few lines in an empty wooden or plastic rectangular frame at least 30 cm on a side, or to rest on the orb of another adult female. All males observed in captivity had been collected less than three hours previously; no male was observed more than once. Each pair's behavior was followed until one of the spiders decamped, or until neither had moved for at least 15 min.

The palps of males frozen in liquid N_2 during copulation failed to remain coupled to females. The positions of palp structures during hematodochal expansion were therefore determined by squeezing the pedipalp of a copulating male near the base with a pair of forceps during maximal hematodochal expansion, cut-

ting the connection to the male, and then plunging the still inflated pedipalp into Duboscq-Brasil fixative (Romeis 1989). Although the angle of the cymbium with the tibia straightened, the hematodochae remained fully inflated, and the positions of the bulbal sclerites were unchanged after the palp was fixed.

The internal anatomy of male and female genitalia was determined using serial semithin sections (1μm) of specimens fixed in ethyl alcohol or Duboscq-Brasil, then embedded in ERL-4206 epoxy resin and stained with methylene blue in an aqueous borax solution (1%) (see Huber 1993). Voucher specimens have been deposited in the Museum of Comparative Zoology at Harvard University, the American Museum of Natural History, and Museo de Zoología of the Universidad de Costa Rica.

RESULTS

Pre-insertion courtship by males.—The term "courtship" is used here to refer to behavior that was repeated both within and between pairs, that obviously resulted in stimuli being received by the other spider, and that had no obvious mechanical function in bringing and keeping the spiders together (i.e., walking toward the female is excluded). The term "copulation" is used to include all genitalic contact between a particular male-female pair until the male left or became immobile. The term "insertion" designates the entrance of the embolus and conductor into the epigynal opening.

Pre-copulatory courtship was both complex and highly variable, and the descriptions below are only a preliminary list of the different types of behavior. The more complex questions of frequencies and sequences of different behaviors are mostly ignored. The substantial variation in the simple presence or absence of particular types of behavior (e.g., Figs. 3, 8) suggests that frequencies, durations, and sequences of different behavior patterns also may be quite variable. The names correpond, when possible, to names used by Robinson & Robinson (1980) in their review of araneid and nephiline courtship behavior. We have illustrated many behavior patterns due to the difficulty we experienced in comparing our observations with those in previous accounts.

Courtship and copulation occur in nature on
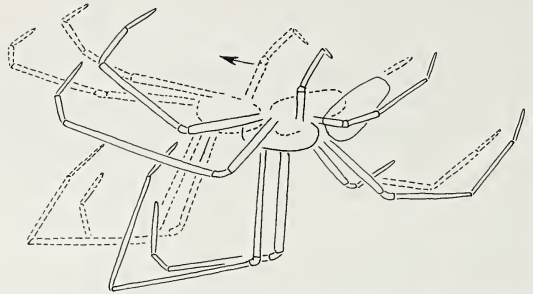
Figure 1.—The forward movement of rocking behavior by a courting male in lateral view (dotted lines follow solid lines by 0.07 sec). The male rocked his body forward and backward by alternately extending and flexing his legs IV.

intact orbs, and on special molting webs (Eberhard et al. 1993). Of the behavior patterns that males performed before copulation, at least seven may function to stimulate females (all were usually performed while the male was on the same line on which the female was resting):

1. Jerk: The male, while facing the female, flexed his anterior legs strongly and quickly (less than 0.1 sec) without releasing the lines they held. The result was a sharp jerk on the web that caused the female's body to swing. These jerks were superficially similar to jerks spiders made in response to prey or other spiders on their webs, and may represent searching behavior rather than courtship. This behavior was similar to that described as "jerk" or "shake" in the courtship of a variety of araneids and nephilines by Robinson & Robinson (1980), and the "jalón" of Castro (1995).

2. Rocking: The male flexed and extended his legs IV rhythmically so that his body rocked backward and up, then forward and down (Fig. 1). In several males vigorous bursts of rocking were accompanied by smaller, more rapid flexes that set the male's entire body quivering briefly. Rocking movements were often performed while the male faced away from the female, but also occasionally while he faced her. This behavior may correspond to "vibración o bamboleo" of Castro (1995). The most similar behavior described by Robinson & Robinson (1980) is the "bounce", but this is apparently an up-and-down rather than a forward-and-backward movement as in *L. mariana.*

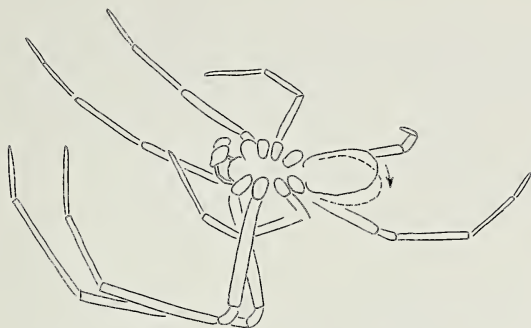Figure 2.—Abdomen bobbing during pre-copulatory courtship (dotted lines follow solid lines by 0.1 sec) in ventral view. The male's abdomen was repeatedly flicked dorsally briefly.

Figure 3.—Ventral view of rapidly alternating palp rubbing movements during pre-copulatory courtship. The posterior movement of the palp (dotted lines on left of drawing, which follow solid lines by 0.07 sec) was followed 0.07 sec later by an anterior movement of the other palp (dotted lines on right follow solid lines there by 0.1 sec).

3. Abdomen bobbing: Abdomen bobbing consisted of quick, dorsally directed flexions of the male's abdomen at the pedicel that lasted about 0.07 sec each (Fig. 2). On some occasions it appeared that the abdomen vibrated as it was twitched, while on others a male flicked his abdomen without causing a general vibration of his body, suggesting that these are two different movements. One common context for abdomen bobbing was at the end of a burst of palp vibration (e.g., Fig. 4). Abdomen bobbing occurred both when the male was facing toward and away from the female. Abdomen bobbing was similar and possibly homologous to rapid "abdomen wagging" movements that occur in a variety of araneid spiders (Robinson & Robinson 1980), and the theridiid *Latrodectus* (Ross & Smith 1979).

4. Palp rubbing: The male moved his pedipalps in brief bursts of alternate anterodorso-posteroventral movements, with the bulb moving from in front of his chelicerae to just ventral to his endites (Fig. 3). Bursts lasted up to several seconds (Fig. 4), and the palps completed a single rub on the order of about one every 0.2–0.3 sec (Fig. 3); in some cases palp movements became progressively more brisk toward the end of each burst of vibration.

Observations at 20× showed that the palps themselves did not usually touch each other during rubbing; in most cases the bristles on each cymbium probably contacted each other, but this was sometimes not the case. The base of each palpal femur rubbed against the retrolateral surface of the chelicera during palpal rubbing, and in some cases one palp was moved while the other was immobile, sup-

porting the possibility that femur-chelicera contact was an important aspect of these movements. Inspection of a male's cuticle with a compound microscope failed, however, to reveal any special structure where the palpal femur contacted the chelicerae.

Palp rubbing movements were termed "oscilación de palpos" by Castro (1995). They appear to be similar to the "palpal scrabbling" described by Robinson & Robinson (1980), but differ in being performed while the male was not in contact with the female. Palp rubbing movements were much more rapid than those of palp cleaning when the male passed his palps through his mouthparts following copulation.

5. Twanging: The male folded his legs III ventrally and strummed the line under which he was walking or hanging repeatedly with alternating lateral movements of the two legs (Fig. 5). Twanging always involved a series of strums, and seemed particularly common at close range, during the final approach to the female prior to cheliceral clasping (Fig. 5). This behavior occurs in many araneids (Gerhardt 1928; Robinson & Robinson 1980; also Blanke 1973, 1986 on *Araneus cucurbitanus* [= *Araneus cucurbitinus* Clerck 1757]; Berry 1987 on *Cyrtophora moluccensis* (Doleschall 1857)). It was noted by Castro (1995) only in *Plesiometa argyra*.

6. Line tapping: The male rested under a line leading toward the female, holding it with
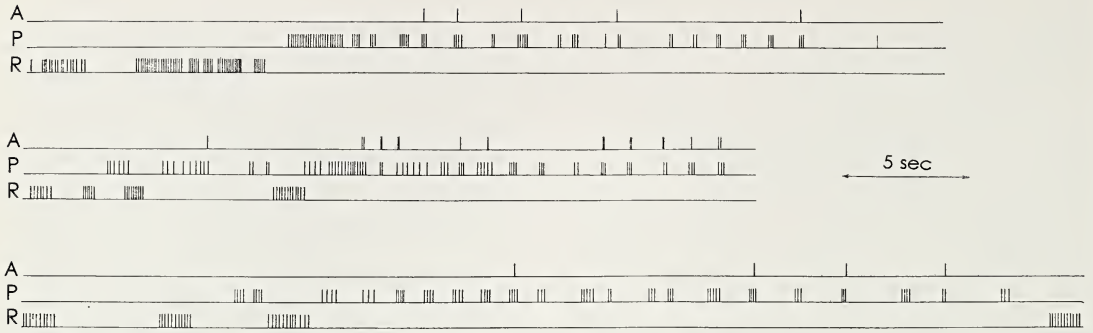
Figure 4.—Patterns of occurrence of abdomen bobbing (A), palp rubbing (P), and rocking (R) in three pre-copulatory courtship sequences in video tapes of one male courting a virgin female. Each vertical line represents a burst of movements. Bursts of rocking and palp rubbing tended to occur in groups. Abdomen bobbing tended to occur in conjunction with palp rubbing, while rocking tended to occur alone.

his partially flexed legs II. Legs I and/or II were held near the line and made quick, mesally directed taps against the line (Fig. 6). The legs apparently did not grasp the line at any time during slapping movements in which the tarsus or metatarsus contacted the line. Usually there were several taps in each series (e.g., Fig. 6). This movement appears not to have been described previously, at least in these terms.

7. *Tapping the female:* The male, especially when interacting with a relatively non-aggressive female, often approached close enough to touch or tap her briefly with his anterior legs, probably with the tarsi or metatarsi. Often after such contact a male turned and moved away several body lengths, then attached his dragline and returned to her along it. Tapping behavior did not seem to be stereotyped with respect to either the parts of the female's body that were contacted or the pattern of movements of the male. This behavior might thus be considered searching or sensory behavior of the male rather than courtship. Nevertheless in some pairs it was the only apparently stimulatory behavior performed by the male be-

Figure 5.—Twanging with one leg III by a courting male (stippled) seen in ventro-lateral view as he approached a female whose chelicerae were already open to clasp his (dotted lines follow solid lines by 0.07 sec). The male used alternate strokes with his legs III to strum the line along which he was moving toward the female.

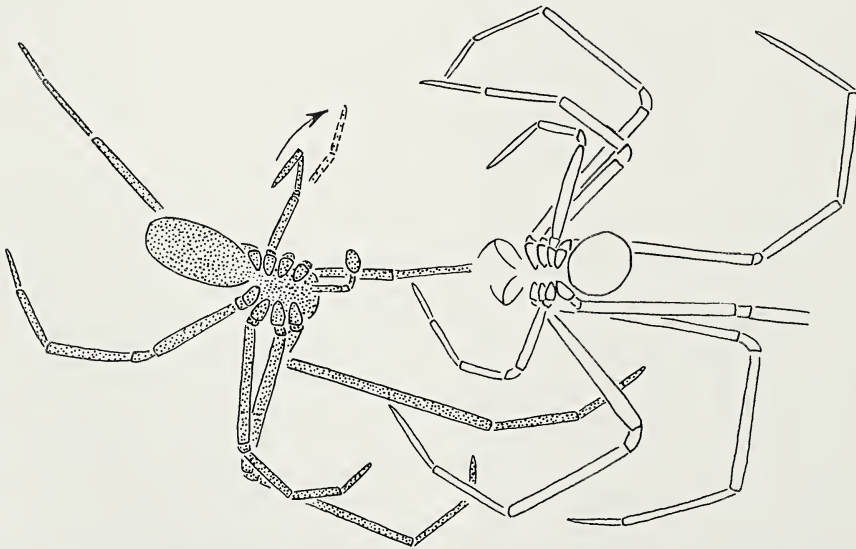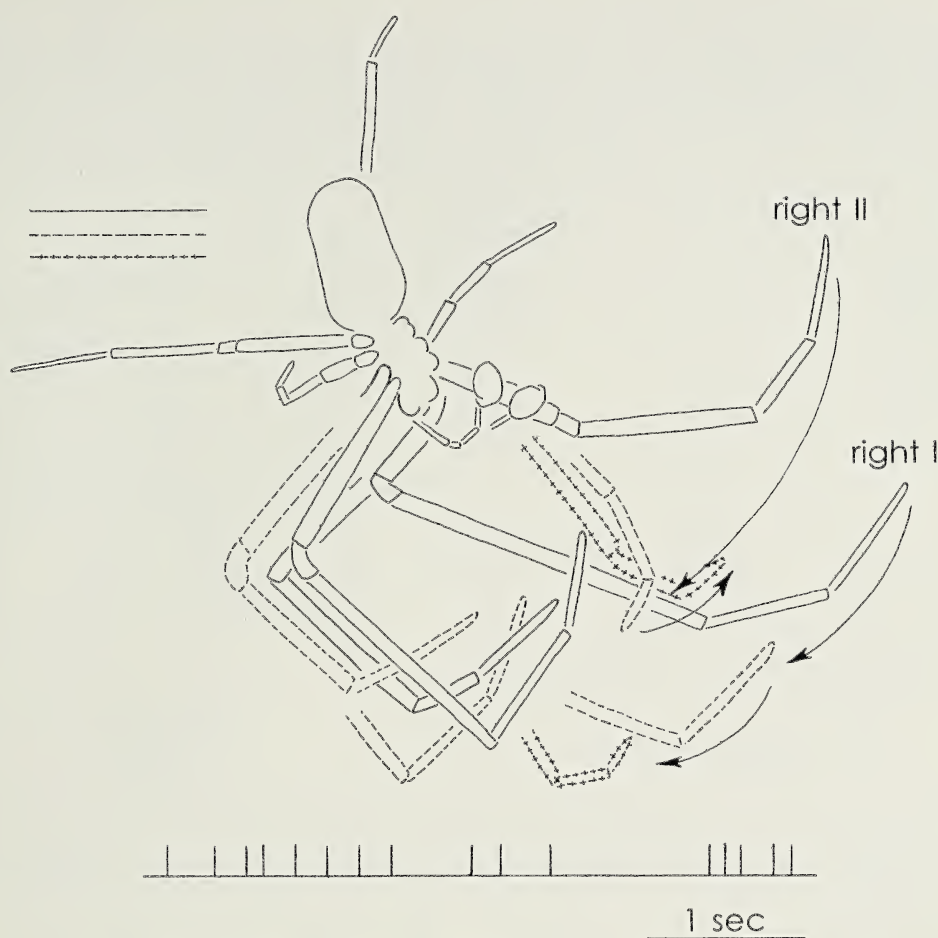Figure 6.—Line tapping during pre-copulatory courtship by a male seen in ventro-lateral view (dotted lines follow solid lines by 0.1 sec). The male's right leg II moved mesally to apparently tap the line on which he was resting, and immediately moved laterally. His right leg I also moved mesally, hitting the line slightly later than leg II. In the graph each vertical bar is a tapping movement.

fore the female assumed the receptive posture and copulated.

Female responses.—We did not attempt to associate particular types of female response with specific male behavior patterns (in most video recordings of male behavior the female was not in view); the general impression was that there was little if any specificity in female responses to particular male signals. Females made three types of responses to male courtship preceding copulation.

1. Turn toward male: The female usually turned to face the male when he approached her from the rear, sometimes however only after the male performed repeated bouts of courtship behavior.

2. Open chelicerae: The female often re-

peatedly opened and closed her chelicerae prior to linking with the male (e.g., Fig. 5); presumably these were intention or exploratory movements associated with cheliceral clasping.

3. Assume mating posture: Just prior to copulation, the female lowered her body while facing directly toward the male, spreading her anterior legs and opening her chelicerae wide, and often flexing her abdomen ventrally in an acceptance posture (Fig. 5). The female clearly bent her abdomen ventrally in 11 of 12 videotaped pairings in which the angle of viewing was adequate to resolve this detail. In two cases the female later bent her abdomen dorsally while the male was attempting to insert his palp, and in one of these pairs he was un-

Figure 7.—Frontal view of the chelicerae of male and female *L. mariana* drawn to the same scale. The anterior surface of the basal segment of the male chelicerae has more setae, and a "ledge" that contacts the basal segment of the female chelicerae (perhaps the distal tooth) while she clasps his chelicerae with hers.

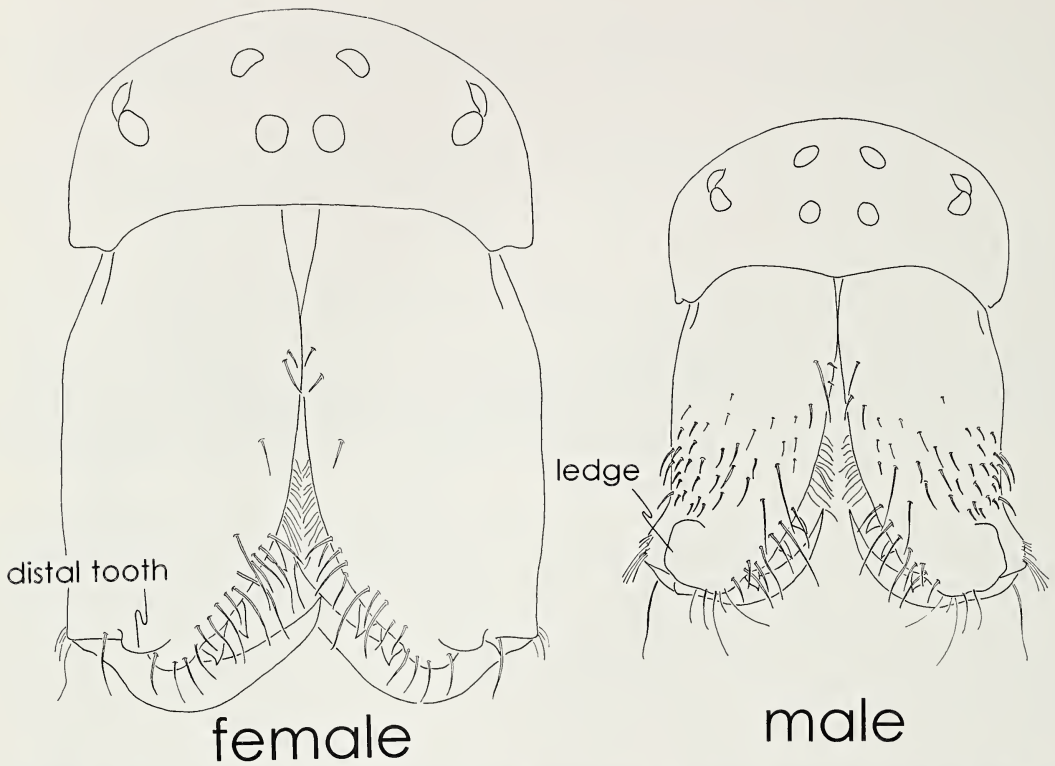able to reach her epigynum as a result. The male often tapped the female with his legs as she lowered herself into position and as she waited there.

Cheliceral clasp.—Relatively stereotyped contact involving both the legs and the chelicerae of the male and the female occurred just prior to copulation. The female always opened her chelicerae wide as the male approached (usually with his own chelicerae closed), and then grasped the distal portions of the basal segments of the male's chelicerae by closing her fangs. The inner surface of her fang clearly pressed against the posterior surface of the male's chelicerae rather than against his endites. The modified "ledge" on the anterior surface of each of the male's chelicerae (Fig. 7) was thus pressed against the distal surface of the basal segment of the female's chelicerae. Observations at 8× with a mirror behind the spiders established that the female cheliceral tooth nearest the insertion of her fang was near the ledge on the male che-

licerae. Unfortunately the abundant hairs on the border of the female chelicerae made it impossible to see the exact position of the female's tooth with respect to the male's ledge. As the cheliceral clasp was being achieved or just after, the male extended one of his pedipalps to rest on the ventral surface of the female's abdomen.

As the two spiders locked chelicerae, the male positioned his legs I and II so that they were in contact with the ventral surfaces of the corresponding legs of the female and tapped against them. Often his legs III were also held against the legs III of the female, contacting their dorsal surfaces. Usually the male contacted the female with the distal portions of his legs I and II (tarsi, metatarsi).

A given pair of spiders often made several cheliceral clasps during a copulation (Fig. 8, Table 1). Between clasps the spiders moved apart, in some cases several body lengths. The male often courted again before each subsequent cheliceral clasp. In some cases the fe-

Table 1.—Characteristics (averages with one standard deviation) of copulations with virgin females and comparisons with copulations with females that had mated once 1–7 days earlier. Frequencies were compared using Chi Squared Tests; other comparisons were made using Mann-Whitney U Tests. Some copulations were observed in more detail than others; this accounts for different sample sizes and missing data. *Significantly different with Mann-Whitney U Test, $P < 0.001$.

	Female Virgin ($n = 24$)	Female Mated ($n = 13$)	P
Duration copulation (min)	17.3 ± 6.1	9.9 ± 13.3	<0.001
Number long insertions	3.5 ± 2.0	0.2 ± 0.6	<0.001
Number bouts of short insertions	6.21 ± 5.2	4.1 ± 3.7	0.201
Number clasps with chelicerae	2.3 ± 1.2	1.7 ± 1.4	0.032
Female pushed palp with leg III at least once	50%	29%	>0.1
Duration long insertions (sec)			
first	109 ± 71 ($n = 24$)		
second	123 ± 67 ($n = 21$)		
third	121 ± 104 ($n = 14$)		
Duration of each bout of short insertions (sec)	40 ± 19 ($n = 41$ bouts, 7 copulations)		
Number hematodochal expansions during each long insertion	57.0 ± 26.1* ($n = 34$ insertions, 7 copulations)		
Number inflations during each bout of short insertions	14.6 ± 7.0* ($n = 41$ bouts, 7 copulations)		

male's behavior just after a pair broke apart appeared to be aggressive, and she made rapid bursts of movement and gave relatively violent jerks on lines running toward the male. The male nevertheless often courted and successfully induced her to approach again (or allow him to approach), and to assume the acceptance posture. Copulations with virgin females were longer, and included more cheliceral clasps than copulations with non-virgins (Table 1).

Copulation.—1. *Leg and abdomen movements:* During copulation males performed at least three behavior patterns seen in pre-insertion courtship: leg tapping with legs I and II, abdomen bobbing, and rocking. During leg tapping the male repeatedly tapped his anterior legs (I, II; sometimes also III) against the female's legs, often on their ventral surfaces (except for legs III). Tapping during copulation differed from pre-copulatory tapping in more consistently involving particular parts of the female's body. Each of the male's legs tapped on the corresponding leg of the female (e.g., male right I on female left I, male right II on female left II, etc.). The order in which

legs tapped varied; frequently (but not always) the right and left legs of a pair alternated.

Bursts of tapping usually lasted several seconds (average 4.5 ±1.2 sec, $n = 13$ bursts by one relatively actively tapping male). Leg tapping occurred during the first moments after the female grasped the male chelicerae and the male attempted to insert his palp, and also nearly always occurred during the withdrawal of one palp and insertion of the other. When, on occasion, there was a pause of a second or more between withdrawal and insertion, leg tapping did not begin until several tenths of a second before the insertion occurred, suggesting that insertion rather than withdrawal is the context for leg tapping. Leg tapping also occurred periodically during long insertions. The rhythm of inflation and deflation of the male's palpal hematodochae was not modified while his legs tapped the female.

Males also performed an additional behavior not seen prior to insertion, bursts of front leg pushing. The male's front four legs were repeatedly extended synchronously against the legs of the female while, in most cases, his legs III and IV were held immobile. Most ex-

Figure 8.—Graphical representation of the sequence of events in four copulations with virgin females. The blocks representing insertions with the two different palps are accompanied by the numbers of hematodochal inflations (inf) (in the case of long insertions), or of insertions (i) and flubs (f) (in the case of short insertions). Long insertions tended to occur earlier, but there was substantial variation in this and other details of copulation.
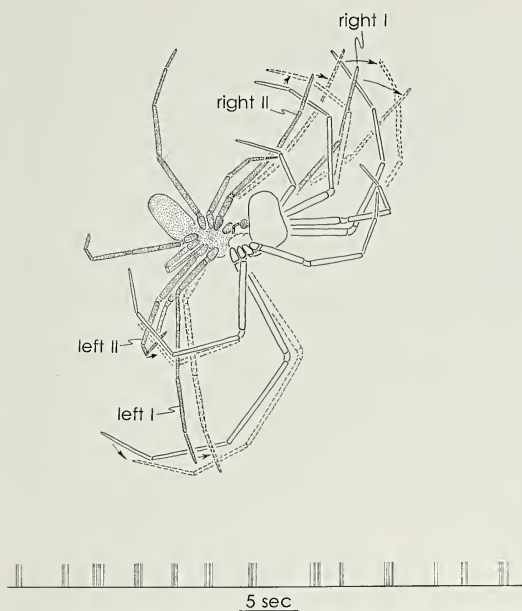
Figure 9.—Rhythmic pushing with the front legs during copulation, seen with male (stippled) in antero-ventral view and the female in postero-lateral view (dotted lines follow solid by 0.07 sec). While the chelicerae were locked, the male's legs I and II contacted the corresponding legs of the female and were extended and moved slightly forward (with respect to the male's body) in synchrony with palpal movements. Legs III and IV of the male were held more or less still (female leg III was out of focus). The graph shows the pattern of pushes by this male (each vertical line is a push). The first push of a series was always stronger than the others.

tension was at the male's femur-patella joint (Fig. 9). Some males pushed only once each time; more commonly, the male made repeated quick series of pushes (Fig. 9). The strength of the pushes varied widely. The number of bursts of pushing during a long insertion ranged from 0–9, and averaged 2.4 for each insertion that had at least one burst of pushing *(n = 8 copulations)*. Bursts of leg pushing began at the same time as the basal hematodocha of the palp was inflated. Deflation, which was much more gradual than inflation, occurred between bursts of pushes.

2. *Movements of the male's genitalia:* Insertion: During each cheliceral clasp, the male extended at least one palp one or more times to contact the female's abdomen. During each extension of a palp the basal hematodocha was expanded one or more times to insert (or attempt to insert) the embolus and conductor

into the female's epigynum. Male palps engaged the female epigynum in two different ways—"long" and "short" insertions. Long insertions usually occurred early in a copulation, and short insertions later, but there were numerous exceptions (e.g., Fig. 8). In a long insertion, each palp usually made only a single long insertion before it was withdrawn from the female's abdomen and the other was inserted (Fig. 8) (occasionally these distinctions were not clear, and the conductor and embolus withdrew from the female following each of the first few inflations of the basal hematodocha, and then remained inserted during subsequent inflations—see descriptions of short insertions below, and Fig. 8). In contrast, short insertions occurred in bursts of several short insertion attempts made by the same palp before it was withdrawn and the other palp was extended to the female's abdomen. The duration of a long insertion averaged over a minute (Table 1), while short insertions lasted only on the order of a second or so. As mentioned above, the first insertions in matings with virgin females were usually of the long type (Fig. 8), while copulations with nonvirgins almost never included long insertions (Table 1). The order of long and short insertions was variable (Fig. 8); sometimes a long insertion occurred after several short insertions had been performed on the same side of the epigynum.

Both long and short insertions began in a similar manner. The palp was extended so that the dorsal surface of the cymbium contacted the ventral surface of the female abdomen just anterior to her epigynum. The trochanter projected ventrally, and the distal portion of the tibia passed near the groove between the inner margins of the female coxae IV, but did not touch it (Figs. 9, 13). At least some of the many setae of the cymbium (Fig. 10), especially those in its basal half, were interlaced among the setae near the female's epigynum (Fig. 14). The cymbium was turned and directed somewhat laterally (e.g., the male's right cymbium was directed to his left, so that its distal tip was just to the female's right of her midline). Although it was difficult to make direct observations, it appeared that the long patellar seta (Fig. 10) often (perhaps always) contacted the cymbium on its inner, concave surface; in some cases this seta was displaced laterally as the basal hematodocha was inflat-
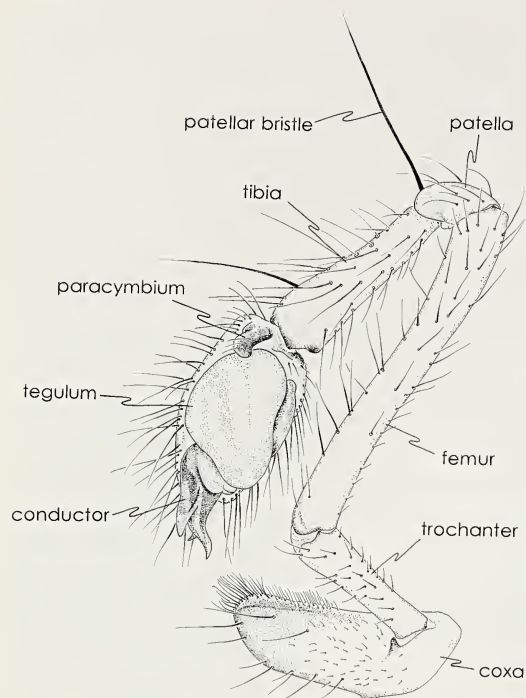
Figure 10.—Entire left palp at rest, showing elongate trochanter, and structures of the bulb (retrolateral view).

ed, confirming that its tip rested on the inner surface of the cymbium.

Inflation: The basal hematodocha was then inflated. The cymbium moved away from the female's ventral surface, and the more distal portions of the palp were displaced away from the cymbium and rotated nearly 180°. During the last portion of this rotation the conductor and embolus moved toward and usually contacted this side of the female's epigynum (i.e., the distal portion of the male's right palp moved to his right, and became inserted into the epigynum on the female's left side). The smaller median hematodocha was inflated during the latter portion of each inflation of the basal hematodocha. It caused the tegulum to move slightly away from the subtegulum, but did not result in any rotation.

In a long insertion, the conductor and embolus, which were driven against the epigynum by the movements produced by hematodochal inflation, remained in contact with the epigynum when the hematodochae partially collapsed. There followed a more-or-less extensive series of approximately simultaneous inflations and collapses of the two hemato-

dochae (Table 1, Fig. 8). During each inflation the distal parts of the palp twisted slightly around the point where the tip of the conductor contacted the entrance of the insemination duct, and the embolus had entered the insemination duct (see below). This movement caused the hook on the conductor process (Fig. 11) to sweep antero-laterally on the female's epigynum until it was arrested just before maximum inflation by hitting the hood on the anterior margin of the atrium (Fig. 14).

During each hematodochal inflation the palp also extended slightly at the femur-patella joint, thus pushing the palp slightly posteriorly on the female's abdomen. The rhythm of expansions was more rapid at the start of a long insertion (avg. 1.1 ±0.34 expansions/sec in the first 20 expansions in the first long insertion of 8 copulations) than later (avg. 0.73 ±0.21 expansions/sec in the last 20 expansions in the same insertions ($P = 0.022$ with Mann-Whitney U Test).

Positions of bulb sclerites: Hematodochal expansions caused the sclerites of the bulb to change positions relative to each other. All major movements seemed to be caused by the expanding basal hematodocha, while the expansion of the median hematodocha apparently only tightened the contact between bulbal sclerites and the epigynum. During the first hematodochal expansion, the base of the embolus was displaced about halfway toward the tip of the thick portion of the conductor, and rested immobile there with its curved tip meshing with the curved surface of the conductor (Fig. 11). Displacement of the base of the embolus was the result of the tegulum being rotated against the paracymbium (Fig. 12). The paracymbium was lodged in a groove on the tegulum, and the rotation caused it to push against and move the base of the embolus. Once this rotation occurred, the base of the embolus did not move during the rest of a given long insertion. The movement of the embolus was made possible by its membranous articulation with the tegulum.

The tip of the embolus projected 155–165 μm beyond the tip of the conductor in three different males. This distance was nearly the same as the distance travelled by the base of the embolus toward the tip of the conductor (Fig. 11), confirming that the movement of the embolus base caused the embolus to be exerted. The tip of the conductor remained
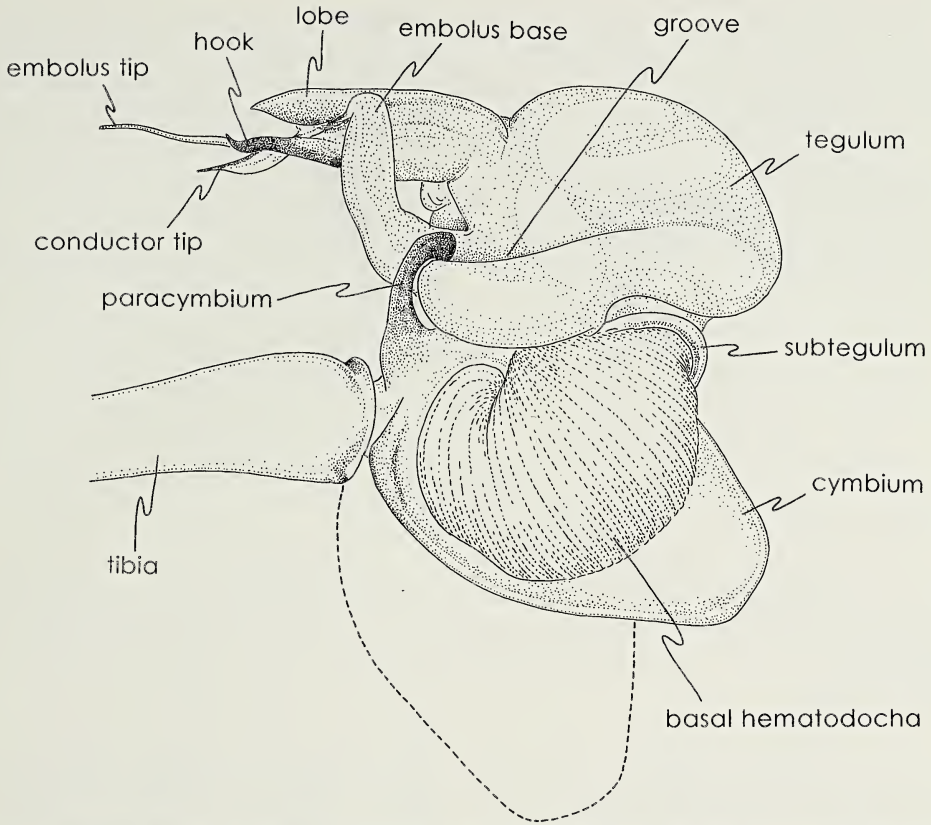
Figure 11.—Ventral view of the distal portion of the right palp with the bulb expanded after being cut from the male and fixed. While the cymbium straightened with respect to its position during insertion (dotted lines) and the hematodochae collapsed (only partially in the case of the basal hematodocha), the distal bulbal structures remained in their natural positions during insertion, with the embolus base erected by the rotation of the tegulum against the paracymbium.

lodged in the entrance of the insemination duct during each long insertion. Thus the tip of the embolus must have passed through the insemination duct and then entered deep into chamber I of the spermatheca (Fig. 15), because the length of the insemination duct of the female was only about 60–80 μm. Since the base of the embolus did not move after the first hematodochal inflation, the embolus presumably remained inserted in chamber I of the spermatheca throughout each long insertion.

After each long insertion, the male withdrew his palp from the female's epigynum. Sometimes he appeared to have difficulty freeing the conductor and embolus, so that only after he had pushed the female with his legs (and sometimes the female had released her cheliceral grip) did his palp come free with a snap.

In the second, short type of insertion, the tips of the conductor and the embolus contacted the epigynum when the basal hematodocha was inflated, as just described, but they rotated back (along with other distal sclerites) to their original position on the cymbium each time the hematodocha collapsed. Usually the same palp was inflated repeatedly before being withdrawn; the number of insertions averaged about five (Table 1, Fig. 8). A burst of short insertions lasted on average less than half as long as a long insertion, and included only about one fourth as many hematodochal inflations (Table 1, Fig. 8). Each time the palpal sclerites rotated to bring the tips of the conductor and the embolus into contact with the epigynum, the base of the embolus was gradually forced toward the tip of the conductor by the paracymbium as in long insertions. The maximum displacement of the base of the

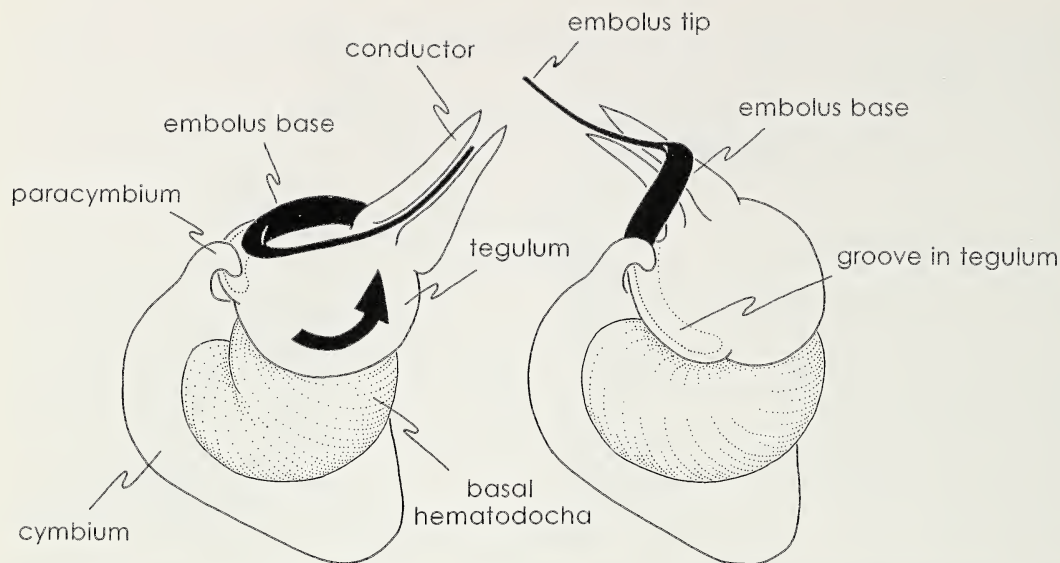Figure 12.—Schematic representation of movements of palpal sclerites that result in projection of the tip of the embolus. The rotation of the tegulum (arrow at left) causes the paracymbium, which is engaged in a groove on the tegulum, to push against the embolus base, and this causes the embolus tip to emerge from the conductor.

embolus was sometimes about the same as that during a long insertion (Fig. 11), but often it moved only part of the way along the conductor. In contrast to long insertions, the base of the embolus returned to its position alongside the tegulum each time the hematodochae collapsed. The median hematodocha also inflated during each inflation cycle of a short insertion, but it was partly hidden; and it was thus not possible to determine exactly when its inflation began with respect to movement of the base of the embolus. It was clear, however, that inflation of this hematodocha continued slightly after the base of the embolus had stopped moving distally.

In some pairs the conductor and embolus pushed so forcefully on the female during each inflation that her abdomen was twisted or deflected perceptibly each time the basal hematodocha inflated (Fig. 13). Judging by these twists in video recordings, the time taken to inflate the hematodocha in one pair was 0.07–0.1 sec; after 0.2 to 0.3 sec, the abdomen gradually sagged back to its original position, remained there for about 0.1 sec more until it was twisted again (Fig. 13).

Flubs: A third type of palpal contact represented apparent failed attempts at insertion ("flubs" in the terminology of Watson 1991). Inflation of the hematodochae caused the tips of the conductor and the embolus to scrape across the face of the epigynum without engaging it as in a successful insertion, or briefly engaging it at an inappropriate site. In one pair, for example, the conductor engaged and was briefly inserted into the slit (Fig. 14) of
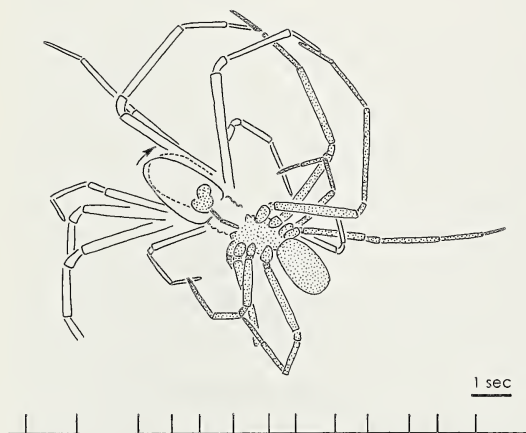

Figure 13.—A short insertion of the right palp of a male (stippled) (in postero-ventral view) caused the female's entire abdomen to be displaced (dotted lines follow solid lines by 0.07 sec). The graph below shows the rhythm of insertions as revealed by displacements of this female's abdomen (each vertical line is a displacement).

the opposite side of the epigynum several times. Flubs were common during bouts of short insertions. In seven copulations (involving 41 bouts of short insertions), there was an average of 8.7 ±4.9 flubs, and 6.6 ±3.7 successful insertions in each bout.

The male often lifted his cymbium from the female's abdomen and then set it down at a slightly different site while making insertion attempts (Fig. 8). Repositioning was more likely to occur following a flub. For instance, 79.6% of 54 repositionings in four copulations occurred following a flub, but only 59% of the 337 insertion attempts in these copulations were flubs ($\chi^2 = 9.46$, $P < 0.01$). Flubs were more common later in a copulation, when short insertions occurred (Fig. 8). The number of flubs varied widely; in eight copulations with virgins the frequency averaged 44%, and ranged from 0% (of 9 insertion attempts) to 73% (of 87 attempts).

3. *Transfer of material to the female and subsequent events:* Sperm were introduced into the large, soft-walled chamber I of the spermatheca (Figs. 14–16) during long insertions, causing it to inflate (compare Figs. 15, 16). The total volume of chamber I of one spermatheca when it was inflated was about 6 $\times$ 10^6 μm^3. In one pair killed and sectioned immediately after a single long insertion, one spermatheca had a mass of sperm (all encapsulated), and the other was still collapsed. The sperm duct of the palp that had been inserted (estimated volume was about 9–11 $\times$ 10^6 μm^3) was about 70% full. The bulb of another male fixed and sectioned just after a complete copulation was almost completely empty.

The dorsal portion of the wall of chamber I of the spermatheca had an array of small pores that were the openings of glands associated with the wall (Fig. 17). In a female fixed 21 min after the end of a long copulation and then sectioned, a dark-staining fluid similar to that in the cells of these glands was present in chamber I near these pores (Fig. 18). Sperm in the portion of chamber I near the pores in the wall had become decapsulated (Fig. 18). The encapsulated sperm in chamber I were accompanied by much less other material than they had been while in the sperm droplet (Fig. 20) or while in the male pedipalp. In two additional females fixed later after copulation (one collected in the field, the other two days after a single copulation) there
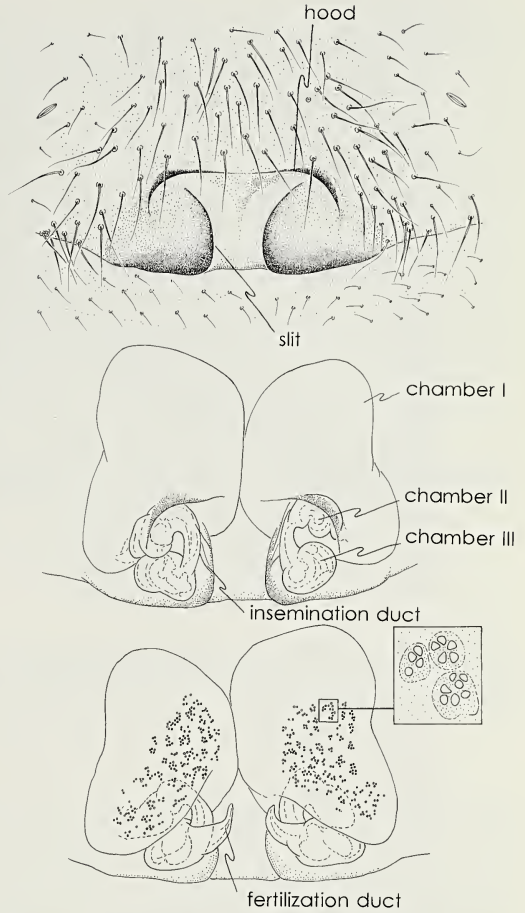
Figure 14.—Top: Female epigynum in ventral view. Middle: vulva of a mated female (cleared in KOH) in ventral view. Bottom: vulva of a mated female (cleared in KOH) in dorsal view (inset shows gland pores in wall of chamber I).

were both encapsulated and decapsulated sperm in chamber I of the spermathecae, and chambers II and III were more tightly packed with decapsulated sperm in small amounts of fluid (Fig. 19). Another female fixed two days after a single copulation also had an additional mass of decapsulated sperm in a small expanded portion of the uterus where the two fertilization ducts emptied. Decapsulated sperm allowed to dry on a glass slide had tails about 17.4 μm long, and curved heads about 7.9 μm long.

During most inflations during short insertions, a viscous white material with an apparent consistency similar to that of toothpaste emerged from the tip of the palp (since no other openings were observed in sections of

chamber I

chamber II

chamber III

epigastric furrow

fertilization duct

insemination duct

atrium
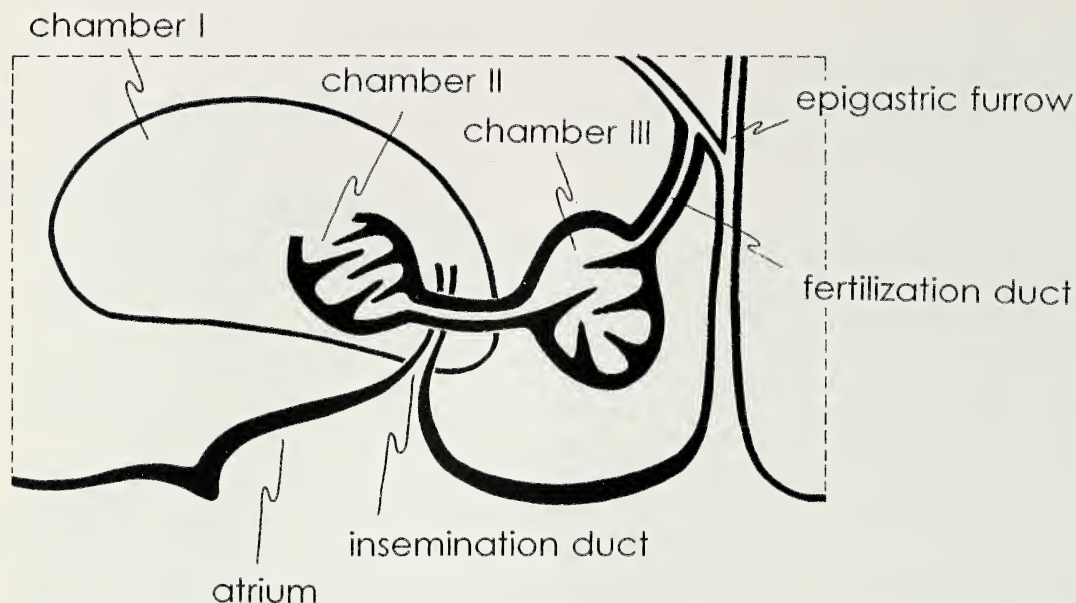
Figure 15.—Schematic lateral view of the internal genitalia of a female (anterior side to the left, ventral side at the bottom). The thin-walled chamber I of the spermatheca, which is collapsed in virgin females, is drawn in its expanded state when filled with sperm and other material (see Fig. 16). Decapsulated sperm occurred in both chamber II and III, as well as in the uterus.

palps, this material presumably emerged from the tip of the embolus). The material emerged while the base of the embolus was being moved by the paracymbium. Since this white material often remained on the outer surface of the epigynum after a copulation was complete, it may be designed to serve as a copulatory plug (or a component of a plug - see below).

In most cases, however, the white material adhered only very poorly to the female. Sometimes it came away still stuck to the male's palp when the embolus and conductor were withdrawn. Often when the tip of the conductor and the embolus were reinserted they dislodged a mass of material that had been deposited previously. During one copulation, for instance, the male more or less filled one side of the atrium with white material three different times, but each time dislodged the accumulation as a result of subsequent insertions. Most copulations with virgin females ended with the female still lacking a plug, even though the male had apparently attempted to deposit one.

In two cases the plug material assumed a more liquid consistency, and flowed into the atrium and presumably at least into the

mouths of the insemination canals, where it condensed into a single, smooth mass that remained in place at the end of copulation. Careful observation of an additional female showed that a similarly liquid plug material had acquired a clearer, less-white appearance and was still very liquid in appearance an hour after copulation ended. The prominent pile of material that had accumulated while the male deposited it had sunk, and had acquired a more level, smooth surface. Similar smooth-surfaced masses were found in the epigyna of many field-collected mature females. Another indication that the material at least sometimes apparently remained liquid in consistency for several minutes was that in some pairs the male performed a long deep insertion on the same side on which he had already deposited material during a shallow insertion.

We had the impression that in the cases in which the female did have a smooth-surfaced plug following copulation, that liquid had emerged from within the female's insemination duct during copulation and combined with the material from the male's palp. When a plug was pulled off the epigynum of a field-collected female, liquid quickly welled up from the insemination ducts and formed a
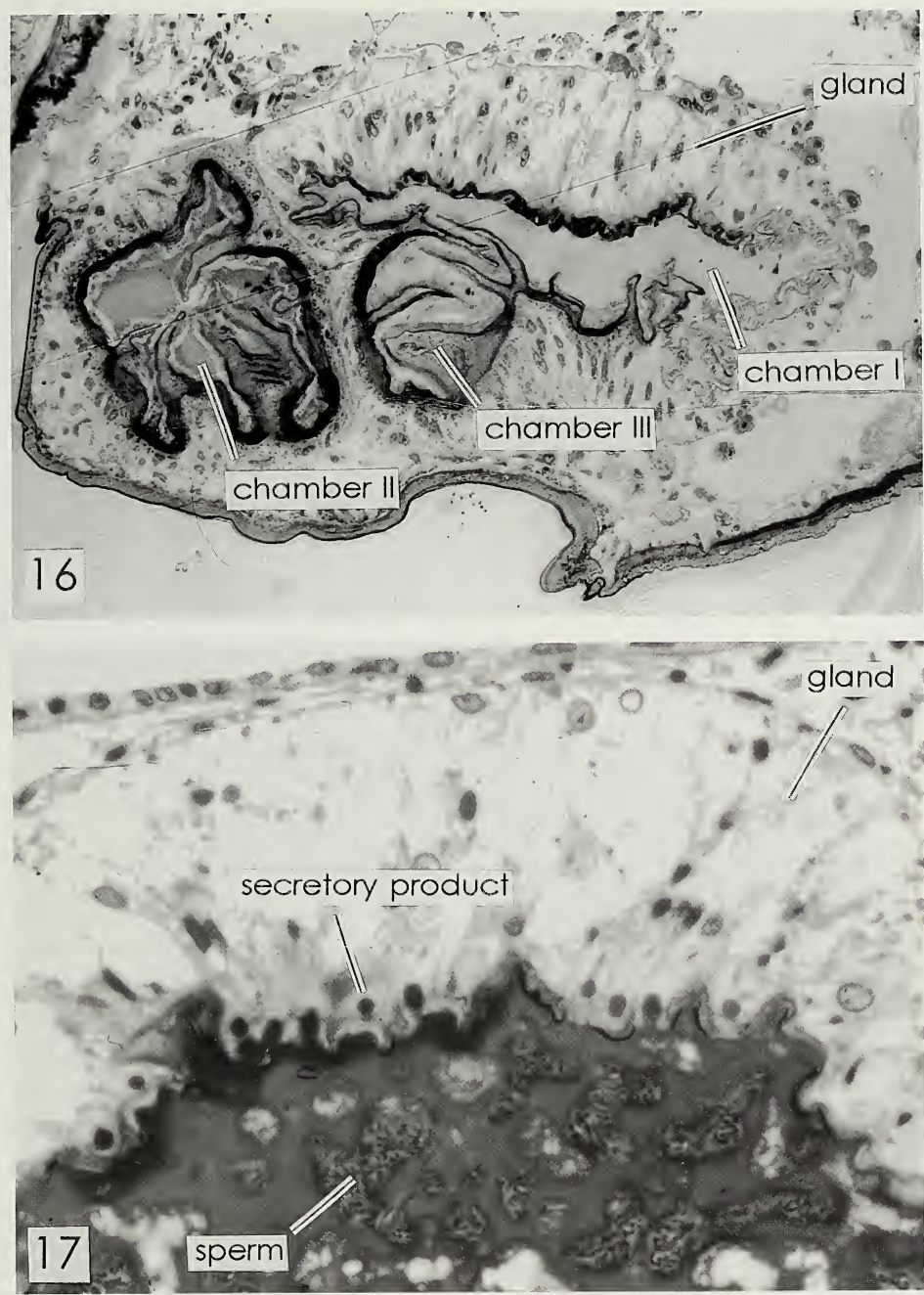
Figures 16, 17.—Internal structure of *Leucauge* abdomen. 16, Saggital section of the abdomen of a virgin female (anterior side to right, ventral side at bottom), showing the collapsed chamber I and its associated gland, and the complex walls of chambers II and III; 17, Section of the dorsal wall of chamber I of the spermatheca, showing glandular cells with a secretory product apparently being transferred to the lumen of the chamber.
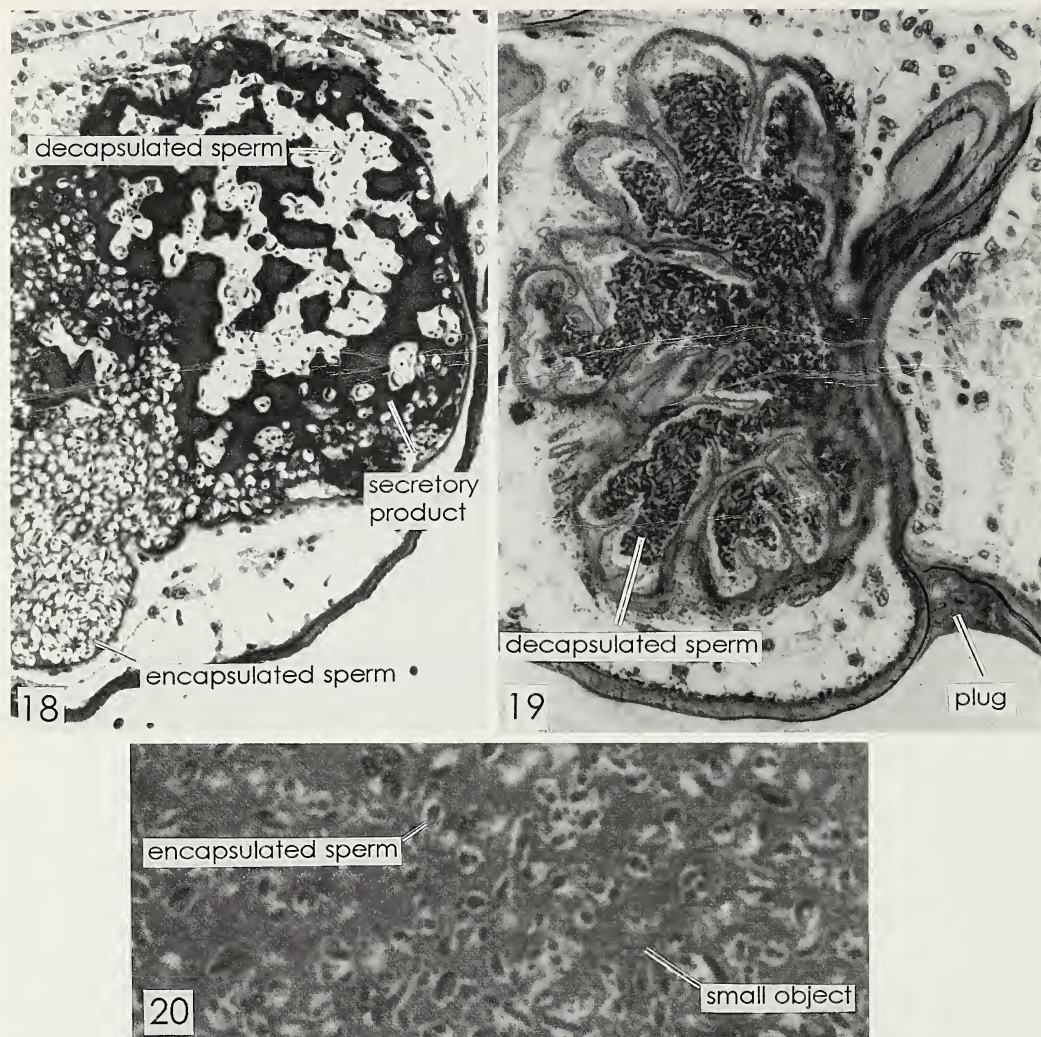
Figures 18–20.—Sperm of *Leucauge*. 18, Saggital section of chamber I of a female shortly after copulation. Sperm in the lower portion of the chamber are still encapsulated and highly concentrated, while sperm in the upper portion, where there is an abundance of a dark-staining material similar to that seen in the gland cells associated with the wall of chamber I, are dispersed and decapsulated; 19, Section of chamber III of the spermatheca of a singly-mated female tightly packed with decapsulated sperm. Plug material (containing encapsulated sperm) is on the surface of the epigynum; 20, The components of a sperm droplet, encapsulated sperm, small round bodies - and a matrix, as seen in a droplet taken from a male's sperm web.

golden crust (as did the liquid which emerged from a puncture wound on the leg). Once the crust formed, the liquid below was withdrawn back into the female's body. Addition of liquid to the male's plug would explain why epigyneal plugs in females collected in the field consistently had smooth outer surfaces and more-or-less filled the atrium of the epigynum, while the material seen being deposited by males during most copulations was in small irregularly-shaped masses of highly viscous material. Of four plugs examined in sections, one clearly contained encapsulated sperm embedded in a matrix, two contained unidentified granules, and one consisted of clear matrix only.

Sperm induction.—Transfer of sperm from the male's gonopore to his palps was observed under a dissecting microscope with four different males 15–60 min after copulation. After

building a "Y" shaped sperm web, the male climbed on top of it and made a small central triangular sheet of fine silk, repeatedly bobbing up and down and apparently drawing silk from his epiandrous glands. Both his legs III were extended ventrally, contacting the sides of the triangle near the bases of their femora. The male then deposited a drop of pearly white liquid at the posterior edge of the sheet (near the base of the isoceles triangle), immediately moved under the sheet, and began taking up this liquid by inserting the tips of his palps (the tips of the embolus and conductor) into it in strict alternation. In three cases the male dipped his palps into the droplet 17–20 times in 30 sec near the start of induction; near the end of the 2–5 min process, the rate of dipping had slowed to 8–15/ 30 sec. One droplet measured 350μm in diameter, giving an estimated volume of 22.4 × 10^6 μm^3. The estimated volume of a single palpal sperm duct, calculated from sections, was approximately 9.5–10.5 × 10^6 μm^3. Thus the sperm droplet probably completely filled the sperm ducts of both palps.

Each immersion lasted only about a second. The tip of the palp touched the anterior surface of the droplet, and then sometimes jerked slightly once or twice as if tapping the droplet. There was an immediate flow of material onto the tip of the palp when the palp first touched the droplet. The liquid appeared to be relatively viscous, and when the tip was pulled away, the surface of the droplet was briefly pulled into a small cone. A small sheath of liquid remained on the tip of the conductor when it was pulled away; there was no perceptible reduction in the amount of this material during the period while the other palp was inserted into the droplet. There were no discernable movements within the palp, or of any of the palpal sclerites at any time during sperm induction.

When the droplet of liquid had almost disappeared, the probing movements of the palps became more insistent, as if the spider sensed that it was sometimes failing to contact the liquid. This impression was reinforced by an inadvertent "experiment". Each time one male pulled his left palp away from a particularly scanty sperm web, nearly the entire sperm droplet adhered to the tip of the palp. Thus every time the right palp was brought into position to take up sperm, there were only tiny droplets left on the sperm web. The right palp of this male clearly probed more actively than did the left throughout sperm induction.

When a recently deposited droplet was examined under a compound microscope and in serial sections, it proved to consist of a liquid matrix containing many small round objects and a smaller number of larger, oval encapsulated sperm (Fig. 20). The sperm ducts in sections of filled male palps also contained encapsulated sperm and smaller granules embedded in a similar matrix. The basal portions of the sperm duct contained the clear homogeneous matrix that filled the entire sperm duct in "empty" male palps before sperm induction.

Failures.—Not all pairings resulted in long palpal insertions; some insertions appeared to be interrupted by the female before the male was finished, and some hematodochal inflations failed to engage the conductor and embolus of the palp in the opening of the female's insemination duct ("flubs"). The apparent reasons for these failures are of special interest, as they suggest the types of "problems" that mating males are under selection to solve.

Probably the most common problem, which was mentioned above, was that the "plug" material did not adhere to the female's epigynum. It was not certain whether this problem was due to the male or to the female, though our incomplete observations suggest that female failure to emit liquid from her insemination ducts was involved.

Another common problem resulted from active female rejection behavior. The female used one of her legs III to kick or push the male's palp away from her epigynum (as also occurs in *Nephila* Leach 1815 and *Cyrtophora* Simon 1864 (Gerhardt 1933; Blanke 1972), or held the palp with the tip of one leg III and flipped her abdomen dorsally, jerking the palp free from the epigynum (Fig. 21). This type of rejection was common (44% of 36 copulations), and usually occurred during short rather than long insertions. It was not significantly more common in copulations with virgin females than with non-virgins (Table 1). In some cases the male succeeded in at least temporarily blocking or in displacing the female's leg III with one of his own legs III, preventing her from contacting his palp. Con-
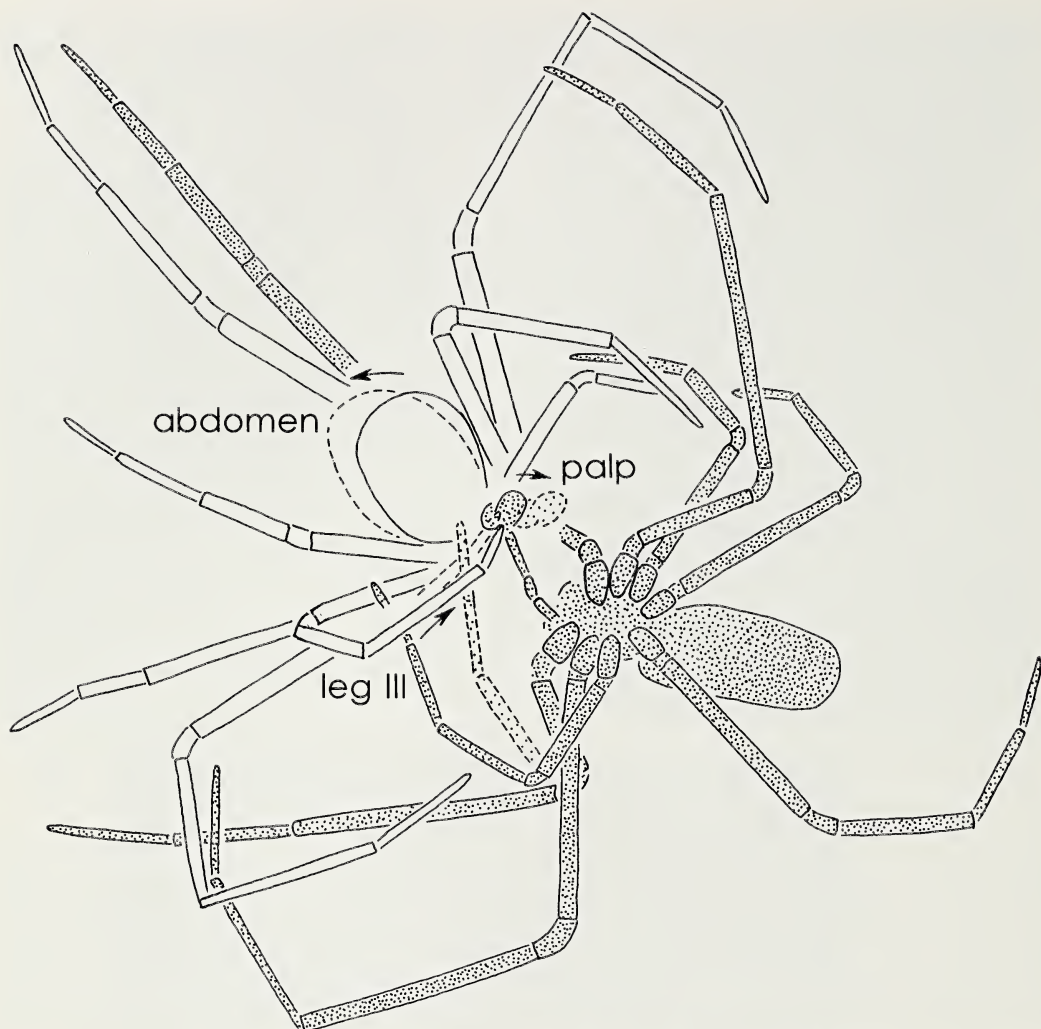
Figure 21.—A female (seen in posterior view) dislodges the palp of a male (stippled) from her epigynum. Although the male moved his leg III to block her (dotted lines follow solid lines by 1.03 sec), the female pushed his palp with her tarsus III (dotted lines follow solid lines by 0.03 sec), and then quickly flexed her abdomen dorsally (dotted lines follow solid lines by 0.03 sec).

certed kicking attempts by females invariably dislodged the palp, however.

Still another problem occurred when the female released her grip on the male's chelicerae and the pair sagged apart while the male attempted to insert his palp. On several occasions the female released the male's chelicerae during a long insertion; in these cases the male simply continued his cycle of hematodochal inflation and deflation, and in two cases the female then resumed her grip while the male continued the long insertion. But in other cases, when the male's palp was not anchored in the female, the separation that oc-

curred when the female released her clasp apparently made it difficult for the male to align his palp properly on her ventral surface and achieve insertion. On one occasion the male responded to being released this way by repeatedly opening and closing his own chelicerae, pressing on the female's fang as he did so. This female eventually opened her chelicerae and the male thrust his own chelicerae between them, thus initiating another cheliceral grasp.

Another possible problem involved the apparent association between flubs and incomplete ventral flexion of the abdomen (see fe-

male acceptance posture above). In one case a relatively small male succeeded in making one insertion, but failed in many subsequent attempts when his palps failed to reach the female's epigynum, and he finally abandoned her. Apparently this male's difficulties were a result of the female failing to bend her abdomen far enough toward him. In several other cases the female appeared to cause flubs, when she deflected her abdomen dorsally during an apparent attempt to make a short insertion.

Overt female aggression toward the male was rare, and did not appear to be a problem, at least during copulation. In one case a female began wrapping the male with silk during a long insertion; the male continued inflating and deflating his hematodochae as before, and escaped readily when the cheliceral clasp ended.

DISCUSSION

Courtship before and during copulation.—The function of male courtship behavior is generally presumed to be to stimulate the female in ways that increase the male's chances of fertilizing her eggs. Demonstration of such a function is not easy, and definitive proof must rely on experimental manipulations of stimuli received by the females. Such manipulations have not been performed with *L. mariana* (nor, indeed, with the large majority of species in which courtship has been studied—see Andersson 1994), so it is necessary to use indirect indicators of probable courtship function. The criteria used here were the following: a) the male's behavior is likely to have caused stimulation of the female; b) the male's behavior was apparently irrelevant to the mechanical problems he experienced in achieving and maintaining genitalic coupling; and c) the male's behavior was repeated during given copulations and in different pairs in relatively stereotyped form. With these criteria, between five and seven types of pre-insertion courtship movements and four types of non-genitalic copulatory courtship occur in *L. mariana*. Copulatory courtship also occurs in *L. venusta* (Walckenaer 1841) (see Castro 1995), and three other unidentified species of *Leucauge* White 1841 (Eberhard 1994), and differs qualitatively among these species (Eberhard 1994).

An additional possible source of stimula-

tion by the male is the substantial displacement of the female abdomen during some palpal insertions (e.g., Fig. 12) (see Coyle & O'Shields 1990 for similar rhythmic movements in the diplurid *Thelochoris karschi* Bösenberg & Lenz 1894, and Huber & Eberhard 1997 on the pholcid *Physocyclus globosus* (Taczanowski 1873)). The number of hematodochal inflations appears to vary dramatically between species, as is expected to often occur in courtship movements under sexual selection (West-Eberhard 1984). Castro (1995) observed an average of over five times more inflations in *L. mariana* (average 103 for 27 copulations) than in *L. venusta* (average 20.8 in 26 copulations) (all copulations were with virgin females). There may also be intraspecific variation in the numbers of inflations, as the average for eight copulations of *L. mariana* in this study was 219 ±71, more than double the average seen in the Mexican population studied by Castro (it is also possible, though seemingly improbable, that the criteria for inflations were not the same in the two studies).

It is not certain whether non-genitalic copulatory courtship in *Leucauge* is an unusual phenomenon among spiders, as might be suggested by the general lack of descriptions of similar behavior in the reviews of courtship and copulation in araneids (Robinson & Robinson 1980) and other spiders (Robinson 1982). There are some reported possible cases of copulatory courtship. For instance, repeated male leg extensions occur during mating in *Nephila* and *Gasteracantha* Sundevall 1833 species (Robinson & Robinson 1980); male abdomen "pumping" occurs in the theriid *Achaearanea wau* Levi, Lubin & Robinson 1982 (Lubin 1986); and rhythmic male abdomen vibrations occur in the pholcid *Physocyclus globosus* (Eberhard 1994; Huber & Eberhard 1997). Apparent non-genitalic copulatory courtship movements by males are known in several species of lycosids (Rovner 1972 on *Lycosa;* G. Stratton pers. comm. on *Hogna* Simon 1885 and *Rabidosa* Roewer 1960). Huber (in press) noted descriptions of apparent copulatory courtship in 31% of 151 species whose behavior was studied by U. Gerhardt.

Underestimates of copulatory courtship are certainly feasible, and in fact one of us (WGE) had previously failed to notice male courtship

movements during observations of several *L. mariana* copulations until after having developed a theoretical reason to suspect that copulatory courtship might occur. Leg tapping is easily misinterpreted as attempts by the male to reposition his legs, until it is noted that the movements occur only in certain contexts, and that the female's legs are usually immobile and not shifting so as to require repositioning by the male. Pushing movements at first seem to be inadvertent extensions of the male's legs associated with changes in internal hemolymph pressure during hematodochal expansions, until it is noted that the third and fourth legs are held completely still, and that some males do not perform pushes while rhythmically inflating their hematodochae. It is sobering to see in one's own observations the strong influence of theory on supposedly objective gathering of empirical data.

An additional aspect of spider mating behavior that may have courtship effects is the often repeated genitalic contact (Huber in press on observations of U. Gerhardt) (for evidence that repeated genitalic contacts can have such a function in other animals, see Eberhard 1996). Patterns of male-female contacts leading to insertions (e.g., cheliceral clasps), of insertions themselves, and of hematodochal expansions during insertions are often complex and variable in different groups of spiders (e.g., Costa & Sotelo 1986 and Stratton et al. 1996 on lycosids; Peaslee & Peck 1983 on an uloborid). The behavior of *L. mariana* was complex in all three respects (Fig. 8).

Secondary sexual modifications of the morphology of male *L. mariana* include a cheliceral process that may be grasped by the female's chelicerae ("ledge" in Fig. 7), and more abundant, stiff setae on the anterior surface of the chelicerae. Similar modifications of the male chelicerae occur in other species of *Leucauge* and in the closely related *Plesiometa argyra* (Castro 1995; W. Eberhard unpubl.). The clasping behavior reported here and by Castro (1995), and the differences among these species suggest that these cheliceral modifications (especially the ledge) may constitute non-genitalic contact courtship devices (Eberhard 1985). It is also possible that they are used as threat devices in male-male battles (especially the setae), as the chelicerae of male *L. mariana* and *P. argyra* may make

contact during intense fights between males (W. Eberhard unpubl.).

Non-virgin females, at least when of the ages used in the present study, were clearly more aggressive toward males, and some pre-insertion courtship may function to reduce the female's aggression. Females are, however, apparently not especially dangerous for males, as no males were killed and one male easily escaped after the female wrapped him with silk. Castro (1995) observed females killing copulating males in captivity, however, in *L. mariana* (4 of 48 copulations), *L. venusta* (1 of 72), and *P. argyra* (3 of 26). Alvarez (1992) also saw a female *P. argyra* kill a copulating male.

This study has documented several processes that females perform during or soon after copulation that could affect a male's chances of fertilizing her eggs. There are several female behavior patterns necessary to just permit a given *L. mariana* copulation to proceed successfully to termination: not kick the palp away from the epigynum; bend the abdomen ventrally so the male palp can reach the epigynum; maintain the cheliceral clasp; and remain immobile rather than walk away or attack the male. Females can and sometimes do interrupt copulations in all of these ways. They may also affect male attempts to plug their epigyna by adding or not adding liquid to the male's plugging material, and could conceivably affect the decapsulation of a male's sperm by varying the amount of glandular product added to chamber I of the spermatheca. There are also several post-copulatory female processes, such as oviposition, and rejection of additional mating attempts (Eberhard 1996) that we did not study and that could affect a male's reproductive success. There is thus an ample range of female responses that male copulatory courtship behavior may serve to induce in *Leucauge*.

The trend for more long palpal insertions to occur in copulations with virgin females resembles copulatory patterns in the theridiid *Achaearanea wau* (see Lubin 1986), and the salticid *Phidippus johnsoni* [= *Dendryphantes johnsoni* (Peckham 1883)] (see Jackson 1980). Entelegyne spiders often show first male sperm precedence (Austad 1984; Christenson 1990; see however Masumoto 1993; Eberhard et al. 1993), and these differences in copulatory behavior may be associated with

sperm precedence patterns. It is not clear, however, why fewer and shorter insertions are more appropriate for matings with non-virgin females. In some spiders very short copulations are just as effective in transferring sperm as much longer copulations (e.g., Jackson & Hallas 1986 on the salticid *Portia* Karsch 1878).

The variation in male courtship behavior both before and during copulation was striking, and resembles similar variability in pre-copulatory courtship in many other orb weavers (Robinson & Robinson 1980). In general, this variability argues against the idea that male courtship functions to inform the female of his species identity. The fact that cross-specific pairing of *L. mariana* and *L. venusta* did not result in initiation of clear pre-copulatory courtship, much less in male-female contact or copulation attempts (Castro 1995), also argues against a species isolating function, especially for copulatory courtship behavior. A more likely explanation, especially for copulatory courtship, is sexual selection (Eberhard 1996), or male attempts to inhibit female aggressive behavior following copulation. Perhaps variety or unpredictability *per se* is stimulatory to the female (e.g., West-Eberhard 1984; Eberhard 1985).

Genital mechanics, sperm transfer, and plugs.—It has been proposed that the relative simplicity of tetragnathid palpal morphology, as compared with the complex morphological features that serve locking and bracing functions in the palps of other araneoid spiders during copulation (e.g., Grasshoff 1973; Huber 1993, 1995), is a mechanical correlate of cheliceral locking between male and female during copulation (Levi 1981; Kraus 1984). The cheliceral clasp is thought to give the male solid purchase on the female's body, eliminating the need for palpal locking mechanisms. Several details of *L. mariana* matings argue against this interpretation: 1) The female rather than the male performs cheliceral clasping. This means that the male is not in control of his supposed purchase on the female. If the female's grasp on the male is sufficiently unreliable (and female *L. mariana* often release males during copulation), then it will not be advantageous for the male to eliminate locking structures on his palps. 2) During insertion the tip of the male's palp is far from the point of cheliceral contact, and his

relatively long palpal trochanter, femur and tibia are not braced in any way by the locked chelicerae or the female's body. In fact, cheliceral clasping results in the base of the male's palp being *farther* from the female's epigynum than in many other araneids. The relatively long distance between the basal segments of the male's palps and the epigynum also means the female must bend her abdomen ventrally to allow copulation, making the male's coupling with the palp even more precarious (an even stronger ventral flexion of the female abdomen must occur to allow copulation in some species of *Tetragnatha* Latreille 1804 and *Pachygnatha* Sundevall 1823 (Gerhardt 1921, 1928; Kaston 1948; Levi 1981; W. Eberhard unpubl.). Sometimes a female *L. mariana* did not bend her abdomen enough for a male to reach her epigynum. 3) The sclerites of the palp of *L. mariana* roll free on the ventral surface of the female abdomen; they rotate dramatically during inflation of the basal hematodocha while the tips of the conductor and embolus are being inserted. These portions of the palp are obviously very *un*braced during copulation. The frequency of failed insertion attempts (flubs) was relatively high in *L. mariana* (just over 50% of all attempts). As mentioned above, in some cases the mispositioning of the palp of *L. mariana* was so substantial that the conductor and the embolus briefly engaged the wrong, ipsilateral side of the epigynum (the ancentral site of insertion - see below).

One puzzling pattern in the flubs of *L. mariana* was that they were more frequent later in copulation, while the very first insertion attempt of a copulation seldom failed. In contrast, "flubs" were most common at first in copulations of *Neriene litigiosa* (Keyserling 1886), and become rarer as the male gradually adjusted his position to that of the female (Watson 1991). It is possible that later insertions in *L. mariana* require more force or a more difficult orientation, or that females were more cooperative at first; but we were not able to discern that these were problems. Another possibility is that "flubs" is a misnomer, and that the behavior serves a stimulatory function as, for instance, may be the case for palpal "drumming" and "scrabbling" in *Nephila* (Robinson & Robinson 1973), and palpal scraping in *Schizocosa* Chamberlin 1904 species (Stratton et al. 1996). The association of

flubs with repositioning of the palp on the female's abdomen suggests, however, that in *L. mariana* flubs do indeed represent mistakes that the male attempts to rectify by repositioning his palp.

We can tentatively assign functional significance to several male genital structures and movements. The conductor hook (Fig. 11), represents the only external mechanical coupling structure of the palp. By lodging against the hood at the anterior edge of the atrium as the basal hematodocha is inflated, the hook serves to arrest the tips of the conductor and embolus at or near the entrance to the insemination duct, and may provide a brace allowing the embolus to be pushed into the female's insemination duct and/or the semen to be pushed into chamber I of the female's spermatheca. The movements of the tegulum against the paracymbium during insertion produce distal displacements of the base of the embolus that result in the insertion of the distal portion of the embolus into the female's insemination duct and spermatheca. The distance that the base of the embolus moved when it was displaced by the paracymbium was similar to the distance that the tip of the embolus projected beyond the tip of the conductor (Fig. 10). Judging by both their morphological relations and the synchronicity of their movements, the movement of the tegulum against the paracymbium was produced by inflation of the median hematodocha.

Transfer of encapsulated and thus immobile sperm to virgin females apparently occurs directly into the first chamber of the spermatheca during the long insertions at the beginning of copulation. Sperm were decapsulated, and thus became potentially mobile, in chamber I. There was additional material associated with sperm in various contexts, including the droplet before it was taken into the palps, in the sperm duct of the palp, in the white material that emerged from the palps during short insertions, in the chambers of the spermatheca, and in the epigynal plug. The origins and fates of these materials are not well understood. The uptake and ejection of the relatively viscous semen is probably produced by resorption and secretion of a material in the palp (Lamoral 1973; Suhm et al. 1995), and it seems likely that some of this material would be present in the lumen of the sperm duct along with the sperm, as has been seen in other spiders (Lamoral 1973; Suhm et al. 1995). Our observations are not sufficient to determine whether the plug material and the small spheres in the sperm fluid (Fig. 16) are the same material. Presumably the plugs serve to impede the access of other males to the female's internal genitalia.

Some of the material associated with sperm inside the female's spermathecae (Fig. 15) is probably derived from the female's spermathecal glands that empty via pores in the dorsal wall of the first spermathecal chamber, because this fluid was not present in the spermathecae of a female fixed soon after copulation, but was present in those of another fixed 21 min after copulation ended. Since only encapsulated sperm were found in the first female, while some sperm had become decapsulated in the other, this female-derived material may have a role in activating the sperm.

Our tentative suggestion that females may make critical contributions of material to the formation of epigynal plugs echoes similar female-active processes in other groups, such as the "insemination reaction" of *Drosophila* (Patterson 1947; Alonso-Pimentel et al. 1994). In apparent contrast with *Drosophila*, plug formation in *L. mariana* is highly variable. It may represent selective female cooperation with the reproductive interests of some males and not others.

Taxonomic implications.—The phylogenetic relations of *Leucauge* with metines, nephilines, and tetragnathines are still uncertain. *Leucauge* has often been included in the Metinae (Simon 1892; Kaston 1948), and linked to *Meta* (C.L. Koch 1836) and *Nephila* (Levi 1980). There are also two possible synapomorphies (dorsal femoral trichobothria, and posterior gut caeca) that link them with tetragnathines (Hormiga et al. 1995). Cheliceral clasping during copulation appears to provide another character supporting a close relationship with tetragnathines.

Cheliceral clasping occurs in *L. mariana* and *L. venusta* (Castro 1995; this study), *L. regnyi* (Alayon 1979 in Castro 1995) and three other unidentified *Leucauge* species (Eberhard 1994). It also occurs in *Plesiometa argyra* (Castro 1995; W. Eberhard unpubl.), and several species in the tetragnathine genera *Tetragnatha* and *Pachygnatha* (Gerhardt 1921, 1923, 1924a, 1928; Osterloh 1922;

Bristowe 1929; Levi 1981; Alvarez 1992; Preston-Mafham & Preston-Mafham 1993; W. Eberhard unpubl. on *T.* sp.). Cheliceral clasps do not occur in *Meta* or *Metellina* (Gerhardt 1921, 1927, 1928; Bristowe 1958) or *Nephila* (Gerhardt 1933; Robinson & Robinson 1973, 1980), nor do they occur in the outgroup Araneinae (e.g., Robinson & Robinson 1980). Thus cheliceral clasping may be a synapomorphy linking *Leucauge* and *Plesiometa* to *Tetragnatha* and *Pachygnatha*. The details of how clasping occurs vary in these groups. In contrast with *Leucauge* spp. and *P. argyra*, in which the female chelicerae open wide and seize those of the male, the males of *Tetragnatha pallescens*, *T. extensa*, and *T.* sp. wedge their chelicerae between those of the female, using a sexually dimorphic cheliceral tooth and a process on the antero-distal surface to (respectively) force the basal segments of the female's chelicerae apart, and to hold her fangs open (Bristowe 1929; Kaston 1948; Preston-Mafham & Preston-Mafham 1993). The clasp of *Pachygnatha clerki* is similar, but the male's kinked fangs also apparently press on and further restrict the movement of the female's fangs (Bristowe 1929). The male of *Pachygnatha degeeri*, in contrast, grasps the basal segments of the female's chelicerae with his, and holds them *closed*.

Two other derived characters supporting this same link between *Leucauge* and tetragnathines are the use of contralateral palps to inseminate the female (Huber & Senglet 1997), and the extraordinarily long pedipalpal trochanters (Fig. 10). Long pedipalpal trochanters are probably linked to cheliceral clasping, as they allow the basal portion of the male's palp to project ventrally, and thus avoid the possible obstacle posed by the female's chelicerae. Cheliceral clasping may have evolved before palpal trochanter elongation, with receptive females bending their abdomens ventrally to facilitate insertion. Or longer palps with long trochanters may have arisen first in groups without cheliceral clasps; long palps occur without cheliceral clasping in, for example, *Filistata* (Gerhardt 1923, 1933), theridiids in the genera *Theridium*, *Teutana*, *Steatoda* (Gerhardt 1924b, 1925, 1923, 1926), and the nesticid *Nesticus* (Huber 1993). In either case, the combination of cheliceral clasping and relatively long palps probably reduces the male's precision in position-

ing his palps just prior to insertion, because of the larger distance at which he must manipulate his palps (see below), and they may thus explain the origin of contralateral insertions. We observed high rates of flubs in *L. mariana* (above).

Our observations of how the palpal structures of *L. mariana* function provide additional links with tetragnathines. The homologous structures in *Pachygnatha clerki* (see Heimer 1982) work in the same way in several respects: 1) the tegulum moved against the paracymbium, 2) the hook of the paracymbium guides the rotation of the tegulum, and 3) this movement causes the embolus to be driven out of the conductor. In *Tetragnatha* sp. the paracymbium is also hooked into a groove on the tegulum (Huber & Senglet 1997; A. Senglet pers. comm.). In contrast, the paracymbium has no direct physical relation with the tegulum or the embolus in either the araneid *Araneus* (Grasshoff 1968), or in members of outgroups such as the linyphiids *Neriene* (van Helsdingen 1969), and *Mynoglenes* (Blest & Pomeroy 1978) and the nesticid *Nesticus* (Huber 1993).

Mating in *Leucauge* spp. occurs on the web rather than on a specially constructed mating thread that replaces web lines (Castro 1995; this study; W. Eberhard unpubl.), and the same is true in *Plesiometa* (Castro 1995; W. Eberhard unpubl.), *Nephila* (Robinson & Robinson 1973, 1980), and *Tetragnatha* (Preston-Mafham & Preston-Mafham 1993). In contrast, many araneines utilize a mating thread (Robinson & Robinson 1980; Robinson 1982). The lack of a mating thread is probably plesiomorphic, however (Robinson & Robinson 1978, 1980). The lack of tarsal rubbing by males during pre-copulatory courtship may also support a link with tetragnathines rather than araneines. This behavior is absent in *Nephila* and associated genera, and is widespread in araneines (Robinson & Robinson 1980) that are only distantly related (Scharff & Coddington 1997). It is not yet clear, however, whether tarsal rubbing constitutes a synapomorphy of this group.

ACKNOWLEDGMENTS

LITERATURE CITED

Alayon, G. 1979. Procesos copulatorios de *Leucauge regnyi* Simon (Araneae: Tetragnathidae). Misc. Zool. Acad. Ciencias Cuba, 4:2–3. [not seen, cited after Castro 1995]

Alonso-Pimentel, H., L.P. Tolbert & W.B. Heed. 1994. Ultrastructural examination of the insemination reaction in *Drosophila*. Cell. Tiss. Res., 275:467–479.

Alvarez del Toro, M. 1992. Arañas de Chiapas. Univ. Auton. Chiapas, Tuxtla Gutierrez, Mexico.

Andersson, M. 1994. Sexual Selection. Princeton Univ. Press, Princeton, New Jersey.

Austad, S. 1984. Evolution of sperm priority patterns in spiders. Pp. 223–250. *In* Sperm Competition and the Evolution of Animal Mating Systems (R. Smith, ed.). Academic Press, New York.

Berry, J.W. 1987. Notes on the life history and behavior of the communal spider *Cyrtophora moluccensis (Doleschall)* (Araneae, Araneidae) in Yap, Caroline Islands. J. Arachnol., 15:309–319.

Blanke, R. 1972. Untersuchungen zur Ökophysiologie und Ökethologie von *Cyrtophora citricola* Forskål (Araneae, Araneidae) in Andalusien. Forma Functio, 5:125–206.

Blanke, R. 1973. Neue Ergebnisse zum Sexualverhalten von *Araneus cucurbitanus* Cl. (Araneae, Araneidae). Forma Functio, 6:279–290.

Blanke, R. 1986. Homologien im Fortpflanzungsverhalten von Kreuzspinnen (Araneae, Araneidae) und deren Interpretation im Kontext von Systematik und der Existenz von Artbarrieren. Actas X Congr. Int. Aracnol. Jaca/España, 1:69–94.

Blest, A.D. & G. Pomeroy. 1978. The sexual behaviour and genital mechanics of three species of *Mynoglenes* (Araneae: Linyphiidae). J. Zool., London., 185:319–340.

Bristowe, W.S. 1929. The mating habits of spiders, with special reference to the problems surrounding sex dimorphism. Proc. Zool. Soc., 21:309–358.

Bristowe, W.S. 1958. The World of Spiders. Collins, London.

Bukowski, T.C. & T.E. Christenson. 1997. Mating in the orbweaving spider *Micrathena gracilis*. II.

Factors influencing copulation and sperm release and storage. Anim. Behav., 53:381–395.

Castro, Teresita de Jesus. 1995. Estudio comparativo del comportamiento reproductor, en las arañas del género *Leucauge* (Araneae, Tetragnathinae), del Soconusco, Chiapas. Thesis Lic., Univ. Ciencias y Artes del Estado de Chiapas, Mexico.

Christenson, T.E. 1990. Natural selection and reproduction: A study of the golden orb-weaving spider, *Nephila clavipes*. Pp. 149–174. *In* Contemporary Issues in Comparative Psychology. (D.A. Dewsbury, ed.). Sinauer; Sunderland, Massachusetts.

Costa, F.G. & R. Sotelo. 1986. Esterotipia y variabilidad del comportamiento copulatorio de *Lycosa malitiosa* Tullgren (Araneae, Lycosidae) a diferentes temperaturas ambientales. Actas X Congr. Int. Arachnol. Jaca, España., 1:131.

Coyle, F.A. & T.C. O'Shields. 1990. Courtship and mating behavior of *Thelochoris karschi* (Araneae, Dipluridae), an African funnel web spider. J. Arachnol., 18:281–296.

Eberhard, W.G. 1985. Sexual Selection and Animal Genitalia. Harvard Univ. Press, Cambridge, Massachusetts.

Eberhard, W.G. 1991. Copulatory courtship in insects. Biol. Rev., 66:1–31.

Eberhard, W.G. 1994. Evidence for widespread courtship during copulation in 131 species of insects and spiders, and implications for cryptic female choice. Evolution, 48:711–733.

Eberhard, W.G. 1996. Female Control: Sexual Selection By Cryptic Female Choice. Princeton Univ. Press, Princeton, New Jersey.

Eberhard, W.G., S. Gomez-Guzman & K. Catley. 1993. Correlation between spermathecal morphology and mating systems in spiders. Biol. J. Linn. Soc., 50:197–209.

Gerhardt, U. 1921. Vergleichende Studien über die Morphologie des männlichen Tasters und die Biologie der Kopulation der Spinnen. Arch. f. Naturgesch., 87 (A, 4):78–247.

Gerhardt, U. 1923. Weitere sexualbiologische Untersuchung an Spinnen. Arch. f. Naturgesch., 89 (A, 10):1–225.

Gerhardt, U. 1924a. Weitere Studien über die Biologie der Spinnen. Arch. f. Naturgesch., 90 (A, 5):85–192.

Gerhardt, U. 1924b. Neue Studien zur Sexualbiologie und zur Bedeutung des sexuellen Grössendimorphismus der Spinnen. Z. Morph. Ökol. Tiere, 1:507–538.

Gerhardt, U. 1925. Neue sexualbiologische Spinnenstudien. Z. Morph. Ökol Tiere, 3:567–618.

Gerhardt, U. 1926. Weitere Untersuchungen zur Biologie der Spinnen. Z. Morph. Ökol. Tiere, 6:1–77.

Gerhardt, U. 1927. Neue biologische Untersuchun-

gen an einheimischen und ausländischen Spinnen. Z. Morph. Ökol. Tiere, 8:96–186.

Gerhardt, U. 1928. Biologische Studien an griechischen, corsischen und deutschen Spinnen. Z. Morph. Ökol. Tiere, 10:576–675.

Gerhardt, U. 1933. Neue Untersuchungen zur Sexualbiologie der Spinnen, inbesondere an Arten der Mittelmeerländer und der Tropen. Z. Morph. Ökol. Tiere, 27:1–75.

Gonzalez, A. 1989. Analysis del comportamiento sexual y producción de ootecas de *Theridion rufipes* (Araneae, Theridiidae). J. Arachnol., 17:129–136.

Gonzalez, A., & A. Armendano. 1995. Comportamiento sexual y producción de ootecas por *Achaearanea tepidariorum* (C.L. Koch) (Araneae, Theridiidae). Rev. Brasiliera Entomol., 39:355–369.

Grasshoff, M. 1968. Morphologische Kriterien als Ausdruck von Artgrenzen bei Radnetzspinnen der Subfamilie Araneinae (Arachnida: Araneae: Araneidae). Abh. Senckenberg Naturf. Ges., 516:1–100.

Grasshoff, M. 1973. Konstruktions- und Funktionsanalyse an Kopulationsorganen einiger Radnetzspinnen. Senckenberg. Naturf. Ges. Frankfurt Main Ber., 24:129–151.

Heimer, S. 1982. Interne Arretierungsmechanismen an den Kopulationsorganen männlicher Spinnen. Staat. Mus. Tierkunde Dresden, 45:35–64.

Hormiga, G., W.G. Eberhard & J.A. Coddington. 1995. Web construction behaviour in Australian *Phonognatha* and the phylogeny of nephiline and tetragnathid spiders (Araneae, Tetragnathidae). Australian J. Zool., 43:313–364.

Huber, B.A. 1993. Genital mechanics and sexual selection in the spider *Nesticus cellulanus* (Araneae: Nesticidae). Canadian J. Zool., 71:2437–2447.

Huber, B.A. 1995. The retrolateral tibial apophysis in spiders - shaped by sexual selection? Zool. J. Linn. Soc., 113:151–163.

Huber, B.A. In press. Spider reproductive behavior: a review of Gerhardt's work from 1911–1933, with implications for sexual selection. Bull. British Arachnol. Soc.

Huber, B.A. & W.G. Eberhard. 1997. Courtship, copulation and genital mechanics in *Physocyclus globosus* (Araneae, Pholcidae). Canadian J. Zool., 74:905–918.

Huber, B.A. & A. Senglet. 1997. Copulation with contralateral insertion in entelegyne spiders (Araneae; Entelegynae; Tetragnathidae). Netherlands J. Zool., 47(1):90–102.

Ibarra, G., O. Jaramillo M. & T. de J. Castro C. 1991. Observaciones sobre el comportamiento reproductor de las arañas del género *Leucauge* (Araneae: Tetragnathidae) del Soconusco, Chiapas, Mexico. Mem. 26 Congr. Nac. Entomol., Veracruz, Mexico: 65–66.

Jackson, R.R. 1980. The mating strategy of *Phidippus johnsoni* (Araneae, Salticidae). II. Sperm competition and the function of copulation. J. Arachnol., 8:217–240.

Jackson, R.R. & S.E.A. Hallas. 1986. Comparative biology of *Portia africana, P. albimana, P. fimbriata, P. labiata,* and *P. schultzi,* araneophagic, web-building jumping spiders (Araneae: Salticidae): utilisation of webs, predatory versatility, and intraspecific interactions. New Zealand J. Zool., 13:423–489.

Jackson, R.R. & A.M. MacNab. 1991. Comparative study of the display and mating behaviour of lyssomanine jumping spiders (Araneae: Salticidae), especially *Asemonea tenuipes, Goleba puella,* and *Lyssomanes viridis.* New Zealand J. Zool., 18:1–23.

Jackson, R.R. & M.E.A. Whitehouse. 1989. Display and mating behaviour of *Thorellia ensifera,* a jumping spider (Araneae: Salticidae) from Singapore. New Zealand J. Zool., 16:1–16.

Kaston, B.J. 1948. Spiders of Connecticut. Bull. State Geol. Nat. Hist. Surv., 70:1–874.

Kraus, O. 1984. Male spider genitalia: evolutionary changes in structure and function. Verh. Naturwiss. Ver. Hamburg, 27:373–382.

Lamoral, B.H. 1973. On the morphology, anatomy, histology and function of the tarsal organ on the pedipalpi of *Palystes castaneus* (Sparassidae, Araneida). Ann. Natal Mus., 21:609–648.

Levi, H.W. 1980. The orb-weaver genus *Mecynogea,* the subfamily Metinae and the genera *Pachygnatha, Glenognatha* and *Azilia* of the subfamily Tetragnathinae North of Mexico (Araneae: Araneidae). Bull. Mus. Comp. Zool., 149:1–74.

Levi, H.W. 1981. The American orb-weaver genera *Dolichognatha* and *Tetragnatha* North of Mexico (Araneae: Araneidae, Tetragnathinae). Bull. Mus. Comp. Zool., 149:271–318.

Lubin, Y.D. 1986. Courtship and mating tactics in a social spider. J. Arachnol., 14:239–257.

Masumoto, T. 1993. The effect of the copulatory plug in the funnel-web spider, *Agelena limbata* (Araneae: Agelenidae). J. Arachnol., 21:55–59.

Osterloh, A. 1922. Beiträge zur Kenntnis des Kopulationsapparates einiger Spinnen. Z. Wiss. Zool., 119:326–421.

Patterson, J.T. 1947. The insemination reaction and its bearing on the problem of speciation in the *mulleri* subgroup. Univ. Texas Publ. Genet., 4720:42–77.

Peaslee, J.E. & W.B. Peck. 1983. The biology of *Octonoba octonarius* (Muma) (Araneae, Uloboridae). J. Arachnol., 11:51–67.

Preston-Mafham, R. & K. Preston-Mafham. 1993. The Encyclopedia of Land Invertebrate Behav-

iour. Massachusetts Inst. Tech. Press, Cambridge, Massachusetts.

Richman, D. & R.R. Jackson. 1992. A review of the ethology of jumping spiders (Araneae, Salticidae). Bull. British Arachnol. Soc., 9:33–37.

Robinson, M.H. 1982. Courtship and mating behavior in spiders. Ann. Rev. Entomol., 27:1–20.

Robinson, M.H. & B. Robinson. 1973. The ecology and behavior of the giant wood spider Nephila maculata (Fabricius) in New Guinea. Smithson. Contrib. Zool., 149:1–76.

Robinson, M.H. & B. Robinson. 1978. Developmental studies of Argiope argentata (Fabricius) and Argiope aemula (Walckenaer). Symp. Zool. Soc. London, 42:31–40.

Robinson, M.H. & B. Robinson. 1980. Comparative studies of the courtship and mating behavior of tropical araneid spiders. Pacific Ins. Monogr., 36:1–218.

Romeis, B. 1989. Mikroskopische Techniken. 17th Ed. Urban and Schwarzenberg, Vienna.

Ross, K. & R.L. Smith. 1979. Aspects of the courtship behavior of the black widow spider, Latrodectus hesperus (Araneae: Theridiidae), with evidence for the existence of contact sex pheromone. J. Arachnol., 7:69–77.

Rovner, J.S. 1972. Copulation in the lycosid spider Lycosa rabida Walckenaer: a quantitative study. Anim. Behav., 20:133–138.

Rovner, J.S. 1973. Copulatory pattern supports generic placement of Schizocosa avida (Walckenaer) (Araneae: Lycosidae). Psyche, 80:245–248.

Rovner, J.S. 1974. Copulation in the lycosid spider Schizocosa saltatrix (Hentz): an analysis of palpal insertion patterns. Anim. Behav., 22:94–99.

Scharff, N. & J.A. Coddington. 1997. A phylogenetic analysis of the orb-weaving spider family Araneidae (Arachnida, Araneae). Zool. J. Linn. Soc., 120:355–434.

Simon, E. 1892. Histoire Naturelle des Araignees. I. 2nd ed. Lib. Encycloped. Roret, Paris. 1084p.

Stratton, G.E., E.A. Hebets, P.R. Miller & G.L. Miller. 1996. Pattern and duration of copulation in wolf spiders (Araneae, Lycosidae). J. Arachnol., 24:186–200.

Suhm, M., K. Thaler & G. Alberti. 1995. Glands in the male palpal organ and the origin of the mating plug in Amaurobius species (Araneae: Amaurobiidae). Zool. Anz., 234:191–199.

Von Helsdingen, P.J. 1969. A reclassification of the spiders of Linyphia Latreille based on the functioning of the genitalia (Araneidae, Linyphiidae). Part I. Linyphia Latreille and Neriene Blackwell. Zool. Verh. (Leiden), 105:1–303.

Watson, P.J. 1991. Multiple paternity as genetic bet hedging in female sierra dome spiders, Linyphia litigiosa (Linyphiidae). Anim. Behav., 41:343–360.

West-Eberhard, M.J. 1984. Sexual selection, social communication, and species specific signals in insects. Pp. 284–324. In Insect communication (R. Lewis, ed.). Academic Press, New York.

A CASE OF BLIND SPIDER'S BUFF?: PREY-CAPTURE BY JUMPING SPIDERS (ARANEAE, SALTICIDAE) IN THE ABSENCE OF VISUAL CUES

P.W. Taylor[1,2], **R.R. Jackson**[1], and **M.W. Robertson**[1,3]:   [1]Department of Zoology, University of Canterbury, P.O. Box 4800, Christchurch 1, New Zealand

ABSTRACT.   Jumping spiders (Salticidae) are well known for their complex visual hunting behavior, but this is the first comparative study investigating their ability to catch prey in the absence of visual cues. When tested with vision occluded inside tubes, where spiders and prey (house flies, *Musca domestica,* and fruit flies, *Drosophila* spp.) could not easily evade each other, each of 42 salticid species tested caught prey in at least one of five different procedures used. Some salticids caught flies less frequently or were less aggressive when tested in petri dishes, where spiders and flies could easily evade each other. For both types of arena and prey, there were significant species differences in both success at prey-capture and tendency to respond aggressively when first contacted by flies. Additionally, there was significant positive correlation between success at catching prey and tendency to act aggressively when first contacted. Salticids resembled short-sighted spiders from other families by only attempting to catch flies when physically contacted, and by rapidly leaning forward ('lunging') to catch prey rather than leaping as they do when visual cues are available. We discuss circumstances in nature when an ability to catch prey in the absence of visual cues might be used by salticids.

Jumping spiders (Salticidae) have visual acuity that far exceeds the abilities of other spiders (Land 1985; Blest et al. 1990) and are well known for their use of vision when communicating (Crane 1949; Clark & Uetz 1994), navigating (Hill 1979; Tarsitano & Jackson 1997) and hunting (Forster 1977, 1979; Jackson & Pollard 1996; Bear & Hasson 1997; Li et al. 1997). Although members of some other spider families do use vision when hunting (e.g., Snelling 1983; Stratton 1984; Jackson et al. 1995), no non-salticid comes close to the refinement of vision-mediated hunting behavior used routinely by salticids. After orienting toward a target, a salticid relies mainly on visual cues when making decisions about whether and how a hunt should proceed (Forster 1977; Jackson & Pollard 1996; Li & Jackson 1996). For example, visual cues about prey identity, size, distance and orientation influence the salticid's speed and direction of approach (Dill 1974; Freed 1984; Jackson & van Olphen 1991; Bear & Hasson 1997). The

salticid slowly creeps up on its prey until close enough for an attack, pauses, and then finally leaps at the prey (Heil 1936; Drees 1952; Forster 1977).

Despite their remarkable adaptation for diurnal activity, salticids appear able to coordinate some activities in darkness. For example, when in darkness, salticids can maintain straight courses by turn-alternation (Taylor 1995) and communicate by vibratory signals transmitted through nests (Richman & Jackson 1992). These non-visual abilities prompt speculation about whether salticids can also catch prey when visual cues are not available. Laboratory studies addressing this issue have yielded conflicting evidence; when tested in large arenas, *Phidippus johnsoni* (Peckham & Peckham 1883) failed to catch prey in the absence of visual cues (Jackson 1977), but *Trite planiceps* Simon 1899 was later found to catch prey when tested in smaller arenas (Forster 1982). *Trite planiceps* lives in dark recesses formed by rolled-up leaves, and adults usually do not build enclosing retreats (see Taylor 1997). Forster (1982) suggested that this species' ability to catch prey in the absence of visual cues is related to its lifestyle promoting frequent encounters with potential prey in darkness. Evaluation of whether *Trite*

[2] Current address: Department of Entomology, The Hebrew University of Jerusalem, P.O. Box 12, Rehovot 76-100 Israel.
[3] Current address: Biology Department, Millikin University, Decatur, Illinois 62522–2084 USA.

planiceps is unusual in its ability to catch prey in the absence of visual cues requires comparative data from a broad array of salticid species from this large and diverse spider family (see Coddington & Levi 1991).

In this paper we investigated the non-visual prey-catching abilities of salticids from 17 subfamilies, including representatives of diverse lifestyles (e.g., foliage-dwellers, ground-dwellers, active hunters, ambush hunters, web-invading araneophages, web-builders, ant-mimics, myrmecophages) and geographic regions (Table 1). For comparative purposes, we also investigated the non-visual prey-catching abilities of some non-salticid hunting spiders (i.e., spiders with comparatively poor eyesight) from the same habitat as *Trite planiceps*.

Because salticid eyes are not sensitive to infra-red light (Blest et al. 1981; Yamashita 1985; Peaslee & Wilson 1989), infra-red video was used to observe the behavior of spiders in the absence of visual cues. This is amongst the first studies to make use of this technology to study the behavior of salticids (see also Taylor 1995).

METHODS

Spiders from laboratory cultures were used (Table 1), excluding individuals that were missing appendages. Standard maintenance procedures were used (Jackson & Hallas 1986). Except during experiments, spiders had *ad libitum* access to adult house flies (*Musca domestica*) or adult fruit flies (*Drosophila melanogaster*) as prey, depending on the spider's size. *Portia* spp., which prefer spiders as prey, had their diets supplemented with various species of spiders, and *Corythalia canosa, Natta rufopicta* and *Zenodorus orbiculatus,* each of which prefers ants, had their diets supplemented with various species of ants. Voucher specimens of all spiders used have been deposited (by RRJ) at the Florida State Collection of Arthropods (Gainesville).

Five different testing procedures were used, but all had the six following elements in common: 1) All tests were carried out during the laboratory light phase (12L:12D), excluding the first and last 2 h. 2) Between tests, arenas were thoroughly washed with water and then ethanol to remove silk and chemical cues that may have accumulated during previous tests. 3) Prior to testing, spiders were kept without

food for 6–8 days. 4) Spiders were tested only once per day. 5) Individual spiders were tested in the dark using only types of prey that they had been observed catching in the light. 6) Spiders were used only once with each prey type in any type of test.

Blinded spiders in horizontal tubes.— Two days after feeding and six days prior to testing, all eyes of the test spider were coated with two or three layers of opaque enamel paint while the spider was subdued under CO_2. A spider and an adult fly (*M. domestica* or vestigial-winged *D. melanogaster*) were placed at opposite ends of a 120 mm-long clear plastic tube plugged by a cork at each end. The spider and fly were separated by a partition placed in a slit at the tube mid-point. Spiders and flies were then left for 5 min to settle down before tests were started. To start a test, the partition was removed so that spiders and flies could move around the entire arena. Spiders were observed for 15 min or until predation occurred.

Spiders 6.0 mm or less in body length were tested in 6.4 mm diameter tubes, whereas spiders 6–8 mm in body length were tested in 7.9 mm diameter tubes. Adult females were used for tests of species in which adult body length was 8 mm or less. Juveniles 6–8 mm in body length were used for species in which adult body length was greater than 8 mm.

Blinded spiders in vertical tubes.—These tests were used primarily for species that failed to catch flies when blinded and in horizontal tubes. Tests using blinded spiders in horizontal tubes and in vertical tubes were identical except for tube orientation. Spiders were placed in the uppermost half of the tube. Because flies tend to move upwards when given the opportunity, this procedure was adopted as a means of promoting more frequent contact between spiders and flies than in tests using horizontal tubes.

Sighted spiders in tubes.—Tests with sighted spiders in tubes were the same as tests using blinded spiders in horizontal tubes except that the arena was made of glass rather than plastic and, instead of blinding the spiders, they were observed using infra-red (IR) video. Tests were staged inside a light-proof cabinet (800 mm high, 1200 mm long, 500 mm deep) illuminated by an infra-red light source (GTE Mini Kat narrow angle IR illuminator) and were observed using a video-

camera that was sensitive to IR light (Burle TC300E CCD). The IR video camera was connected to a monitor positioned outside the cabinet so that behavior of spiders could be observed. Because the video field of view encompassed the whole arena there was no need to track the spiders and flies as they moved about during experiments. The light-proof cabinet had sleeves (500 mm long), consisting of a double layer of heavy black satin, attached to a 150 mm diameter hole in the wall so that the experimenter could reach in to remove the partition (i.e., begin tests) without allowing light to enter.

Rather than varying the tube diameter with spider size, only adult spiders were used and all spiders were tested in tubes that were 100 mm in length and 11 mm in internal diameter. Fruit flies used were fully winged *Drosophila immigrans* instead of vestigial winged *D. melanogaster*. *Drosophila immigrans* is larger and more active in darkness than is *D. melanogaster,* and the spiders and flies contacted each other more frequently when this species was used in preliminary tests. Instead of adjusting prey size to spider size, all spiders were tested using a 'standard fruit fly' 2.5–3 mm in body length or a 'standard house fly' 7–8 mm in body length. After placing a fly and a spider at opposite ends of the tube with the partition in place, the tube was placed horizontally in the light proof cabinet. The partition was removed in IR light after the spiders had been in IR light for a 5 min settling-down period. Each test lasted 15 min or until the spider caught the fly.

In preliminary tests, individual spiders responded to contact with the flies in one of several different ways. A spider might respond in an apparently aggressive manner; it might actually lunge at the fly (rapidly lean forward by extending Legs III and IV, tarsi of these legs remaining on the substrate) and attempt to grasp it with the front legs, or it might carry out apparent preliminaries to lunges, such as orienting toward the fly or raising its front legs. These responses were collectively termed 'confront'. Alternatively, a spider might respond in an apparently less aggressive manner; it might run, walk, or leap (all tarsi leave the substrate) away from the fly, turn away from the fly without stepping, or lean away from the fly by flexing legs on the side opposite to the fly. These responses

were collectively termed 'avoid'. Whether spiders and flies physically contacted each other during the 15 min testing period was recorded and responses of spiders to first contact with the fly were recorded as either confront or avoid. The tendency to confront, rather than avoid, flies provided a general measure of 'aggressiveness'.

If flies were grasped and then released, or if they broke free from spiders during tests, these spiders and flies were kept in IR light for a further 60 min after the 15 min testing period ended. This enabled us to investigate whether the flies died and, if the flies died, whether the spiders later picked up the dead flies and ate them. When flies died after being bitten, this was recorded as a capture.

Sighted spiders in petri dishes.—The arena used here was a plastic petri dish (85 mm diameter) with a plastic tube (30 mm long, 7 mm internal diameter) glued onto a hole in the wall. A standard house fly (i.e., 7–8 mm body length) was placed into the tube. A partition inserted into a slit at the petri dish end of the tube and a wooden plunger inserted into the other end of the tube prevented the fly's escape. Next, the test spider was placed in the petri dish and the arena was placed into the light-proof cabinet. After a 5 min settling-down period, the partition was removed. The entry of the fly into the dish defined the beginning of the test. As soon as the test began, the plunger was depressed so that neither the spider nor the fly could leave the petri dish. Tests lasted 15 min or until prey capture, and were observed using IR video (see above). These tests are the closest approximation in the present study to the procedures used by Jackson (1977) and Forster (1982) to investigate non-visual predation in the salticids *Phidippus johnsoni* and *Trite planiceps,* respectively, but with the improvement of being able to observe the behavior of the spiders.

Sighted spiders in darkness *vs.* light.—In these tests, we assessed differences in the frequency with which individual spiders caught flies in darkness *versus* light. The general procedure resembled tests using blinded spiders in horizontal tubes except that spiders were not blinded. Instead, each individual spider was tested once in the light and once in darkness on successive days (in random order). To begin tests in darkness, the tubes were placed horizontally in a light-proof cabinet as soon

Table 1.—Spiders tested for ability to catch prey in the absence of visual cues.

	Subfamily (Family)[1]	Origin	Typical adult body length (mm)
Salticids			
Asemonea tenuipes O. P. Cambridge 1869	Lyssomaninae	Sri Lanka	4
Bavia aericeps Simon 1877	Thiodininae	Australia (Queensland)	12
Corythalia canosa (Walckenaer 1837)	Plexippinae	USA (Florida)	6
Cosmophasis bitaeniata (Keyserling 1882)	Heliophaninae	Australia (Queensland)	6
Cosmophasis micarioides (L. Koch 1880)	Heliophaninae	Australia (Queensland)	7
Cosmophasis sp.	Heliophaninae	Philippines	7
Cyrba ocellata (Kroneberg 1875)	Spartaeinae	Sri Lanka	5
Epeus sp. 1	Hyllinae	Singapore	8
Epeus sp. 2	Hyllinae	Philippines	8
Eris marginata (Walckenaer 1837)	Dendryphantinae	USA	6
Euophrys parvula Bryant 1905	Euophrynae	New Zealand	6
Euryattus sp.	Cytaeinae	Australia (Queensland)	8
Hasarius adansoni (Andouin 1827)	Hasariinae	Australia (Queensland)	6
Helpis minitabunda (L. Koch 1880)	Astianae	New Zealand	7
Hentzia mitrata (Hentz 1846)	Dendryphantinae	USA (North Carolina)	5
Holoplatys planissima (L. Koch 1879)	Marpissinae	New Zealand	8
Holoplatys sp.	Marpissinae	New Zealand	5
Jacksonoides queenslandicus Wanless 1988	Astianae	Australia (Queensland)	7
Lyssomanes viridis (Walckenaer 1837)	Lyssomaninae	USA (Florida)	6
Marpissa marina Goyen 1892	Marpissinae	New Zealand	8
Menemerus bivattatus (Dufour 1831)	Marpissinae	Australia (Queensland)	5
Mogrus dumicola (O. P. Cambridge 1872)	Dendryphantinae	Israel	8
Mopsus mormon Karsch 1878	Thyeninae	Australia (Queensland)	12
Myrmarachne lupata L. Koch 1879	Myrmarachninae	Australia (Queensland)	5
Natta rufopicta Simon 1901	Heliophaninae	Kenya	5
Phidippus johnsoni (Peckham & Peckham 1883)	Dendryphantinae	USA (California)	9
Phidippus sp. 1	Dendryphantinae	USA (Arizona)	9
Phidippus sp. 2	Dendryphantinae	USA (Texas)	9
Plexippus calcaratus Karsch 1880	Plexippinae	Australia (Queensland)	10
Portia africana (Simon 1886)	Spartaeinae	Kenya	8
Portia fimbriata (Doleschall 1859)	Spartaeinae	Australia (Queensland)	8
Portia labiata (Thorell 1882)	Spartaeinae	Sri Lanka, Philippines	8

Table 1.—Continued.

	Subfamily (Family[1])	Origin	Typical adult body length (mm)
Portia schultzi Karsch 1878	Spartaeinae	Kenya	7
Simaetha paetula (Keyserling 1882)	Simaetheae	Australia (Queensland)	8
Tauala lepidus Wanless 1988	Astianae	Australia (Queensland)	7
Thiania bhamoensis Thorell 1887	Itatinae	Singapore	5
Thorellia ensifera Thorell 1887	Spilarginae	Singapore	5
Trite auricoma Urquhart 1885	Cytaeinae	New Zealand	9
Trite planiceps Simon 1899	Cytaeinae	New Zealand	10
Tularosa plumosa de Lessert 1925	Hasariinae	Kenya	5
Viciria praemandibularis (Hasselt 1893)	Hyllinae	Singapore	10
Zenodorus orbiculatus (Keyserling 1881)	Euophrynae	Australia (Queensland)	4
Non-salticids			
Cheiracanthium stratioticum L. Koch 1873	Clubionidae[1]	New Zealand	8
Clubiona cambridgei L. Koch 1873	Clubionidae[1]	New Zealand	8
Dysdera crocata C. L. Koch 1838	Dysderidae[1]	New Zealand	10
Supunna picta (L. Koch 1873)	Clubionidae[1]	New Zealand	8
Taieria erebus (L. Koch 1873)	Gnaphosidae[1]	New Zealand	7

Table 2.—Number of individuals tested (n) and percentage that captured flies (C) during tests using blinded spiders in tubes. Species marked with a superscript 1 are non-salticids.

	Tubes horizontal		Tubes vertical	
	n	C	n	C
Tests using fruit flies				
Clubiona cambridgei[1]	9	66	6	66
Bavia aericeps	12	17	—	—
Corythalia canosa	9	22	—	—
Cosmophasis micarioides	6	17	—	—
Epeus sp. 1	7	14	—	—
Euophrys parvula	12	33	—	—
Hasarius adansoni	8	13	—	—
Helpis minitabunda	8	24	—	—
Holoplatys sp.	7	0	9	22
Jacksonoides queenslandicus	10	0	14	14
Lyssomanes viridis	10	0	11	9
Marpissa marina	7	0	7	14
Mopsus mormon	10	10	—	—
Myrmarachne lupata	6	0	5	20
Phidippus johnsoni	12	0	11	9
Plexippus calcarata	11	27	—	—
Portia labiata	7	0	8	13
Tauala lepidus	6	17	—	—
Thiania bhamoensis	7	14	—	—
Trite auricoma	15	20	—	—
Trite planiceps	10	40	7	43
Zenodorus orbiculatus	6	17	—	—
Tests using house flies				
Clubiona cambridgei[1]	4	100	—	—
Bavia aericeps	5	20	—	—
Euophrys parvula	5	20	—	—
Helpis minitabunda	4	0	5	20
Jacksonoides queenslandicus	9	0	10	20
Marpissa marina	8	38	7	14
Mopsus mormon	4	25	—	—
Phidippus johnsoni	5	0	10	10
Tauala lepidus	7	43	—	—
Trite auricoma	8	38	—	—
Trite planiceps	10	40	—	—

as the barrier was removed, and then left for 24 h. At the end of tests, dead flies were inspected for fang holes and mastication to confirm that they had been bitten by the spider.

Statistical methods.—Tests of independence in 2×2 contingency tables were carried out using Fisher's exact test, whereas tests in larger tables were carried out using χ^2 (excluding species for which $n < 10$). Tests of association were carried out using Spearman's rank correlations (excluding species for which $n < 10$). McNemar's test for significance of changes (Sokal & Rohlf 1981) was used to compare frequency data obtained from se-

quential testing of individuals in darkness and light.

RESULTS

Success at non-visual predation.—Each of the 47 species tested (42 salticids and 5 non-salticids) caught prey in the absence of visual cues in at least one type of test (Tables 2–4). There was no evidence of differences among salticid species in how frequently they caught prey in darkness when blinded (in horizontal or vertical tubes) or when sighted and tested for 24 h (for all test types, $P > 0.1$). However, there was significant variation

among salticid species during tests using sighted spiders in tubes (fruit flies, $\chi^2 = 95.06$, 14 df, $P < 0.001$; house flies, $\chi^2 = 103.30$, 17 df, $P < 0.001$) and tests using sighted spiders in petri dishes (house flies, $\chi^2 = 154.80$, 13 df, $P < 0.001$). All species of non-salticids caught flies in all types of test, and there was no evidence that they differed in capture frequency in any type of test (for all test types, $P > 0.1$).

In experiments testing individual spider's success at catching flies in darkness and in light, all salticids caught fruit flies and house flies less frequently in the dark than in the light (Table 4). In contrast, there was no evidence that absence of light affected how often *Clubiona cambridgei,* the non-salticid tested, caught flies (Table 4).

Some sighted spiders caught flies immediately following the first physical contact with the flies ('immediate captures'). During tests in tubes using fruit flies as prey, immediate captures were made by the non-salticids *Clubiona cambridgei* (16 of 24 captures recorded), *Dysdera crocata* (2 of 10), *Supunna picta* (6 of 9) and *Taieria erebus* (4 of 8) as well as the salticids *Euophrys parvula* (1 of 10), *Helpis minitabunda* (1 of 7), *Mogrus dumicola* (1 of 4) and *Phidippus* sp. 1 (1 of 5); during tests in tubes using house flies as prey, they were made by the non-salticids *Cheiracanthium stratioticum* (3 of 11), *Clubiona cambridgei* (19 of 45), *Dysdera crocata* (2 of 13), and *Supunna picta* (6 of 16) as well as the salticids *Corythalia canosa* (1 of 5), *Euophrys parvula* (1 of 18), *Phidippus* sp. 2 (1 of 8), *Portia africana* (1 of 4) and *Trite planiceps* (5 of 18); during tests in petri dishes using house flies as prey, the non-salticids *Clubiona cambridgei* (8 of 20), *Dysdera crocata* (3 of 10), and *Supunna picta* (4 of 15) made immediate captures, whereas *Trite planiceps* (9 of 37) was the only salticid observed to make immediate captures in these tests.

Associations amongst spider size, aggressiveness and success at prey capture.—Salticid species varied in the frequency with which they confronted fruit flies and house flies when first contacted ('aggressiveness') during tests in tubes (fruit flies, $\chi^2 = 63.20$, 13 df, $P < 0.001$; house flies, $\chi^2 = 79.34$, 16 df, $P < 0.001$) and in petri dishes (house flies, $\chi^2 = 109.40$, 13 df, $P < 0.001$) (see Table 3). In contrast, all of the non-salticids were sim-

ilar in that they usually confronted flies when first contacted (see Table 3), and there was no evidence of species variation in frequency of confrontation by non-salticids during any test type (for all test types, $P > 0.1$).

Salticid species that often confronted flies when first contacted tended to catch flies more frequently than species that rarely confronted flies during tests of sighted spiders in tubes (fruit flies, $r_s = 0.6677$, 13 df, $P < 0.01$; house flies, $r_s = 0.6779$, 16 df, $P < 0.01$) and tests of sighted spiders in petri dishes (house flies, $r_s = 0.5965$, 13 df, $P < 0.05$).

During tests with fruit flies in tubes, *Trite auricoma* individuals that confronted flies were more likely to catch the prey than were conspecifics that avoided flies when first contacted ($P < 0.05$). For all other species in all tests, there was no evidence that likelihood of catching flies was related to an individual spider's response when first contacted (for all species in all test types, $P > 0.1$). There was no evidence of relationship between size of salticid species (Table 1) and the proportion of individuals that confronted or caught flies in tests of sighted spiders in tubes or in petri dishes using either prey type (for all test types, $P > 0.1$).

Comparison of arenas used with sighted spiders.—For the following salticids, house flies were captured less frequently in the petri dish arena than in the tube arena (Table 3): *Cosmophasis* sp. ($P < 0.05$), *Euophrys parvula* ($P < 0.001$), *Helpis minitabunda* ($P < 0.001$), *Marpissa marina* ($P < 0.001$), *Mopsus mormon* ($P < 0.05$), *Portia labiata* ($P < 0.001$), *Portia shultzi* ($P < 0.05$), *Trite auricoma* ($P < 0.01$) and *Trite planiceps* ($P < 0.01$). However, there was no evidence for any non-salticid species that frequency of prey-capture by was different in these two types of tests (for all species, $P > 0.1$).

Some salticids confronted house flies less frequently when tested in petri dishes rather than in tubes (Table 3): *Corythalia canosa* ($P < 0.05$), *Euophrys parvula* ($P < 0.001$), *Marpissa marina* ($P < 0.001$) and *Portia labiata* ($P = 0.057$). However, there was no evidence for any non-salticid species that frequency of confrontation was different in these two types of test nor was there evidence that frequency of contact with house flies was different in these two types of test for any salticid or non-salticid (for all species, $P > 0.1$).

Table 3.—Behavior and prey-capture success of sighted spiders in tubes and in petri dishes. Species marked with a superscript 1 are non-salticids. 'Contact' is the percentage of *n* that contacted the fly (see text). 'Confront' is the percentage of individuals that confronted, rather than avoided, the fly (see text) immediately after first contact and 'Capture' is the percentage of *n* that captured the fly.

	n	Contact	Confront	Capture
Tests in tubes using fruit flies as prey				
Cheiracanthium stratioticum[1]	28	50	86	50
Clubiona cambridgei[1]	33	73	92	73
Dysdera crocata[1]	18	72	62	56
Supunna picta[1]	15	73	82	60
Taieria erebus[1]	16	63	70	50
Bavia aericeps	15	73	9	0
Corythalia canosa	17	53	0	12
Cosmophasis bitaeniata	4	75	33	50
Cosmophasis sp.	12	83	0	42
Epeus sp. 2	3	67	0	0
Eris marginata	5	100	0	0
Euophrys parvula	22	64	57	45
Helpis minitabunda	46	87	8	15
Holoplatys planissima	8	50	25	0
Jacksonoides queenslandicus	20	80	0	0
Lyssomanes viridis	33	70	0	12
Marpissa marina	28	93	23	46
Mogrus dumicola	26	42	9	15
Mopsus mormon	8	88	14	0
Phidippus sp. 1	13	85	45	38
Phidippus sp. 2	9	89	13	33
Portia fimbriata	22	64	0	5
Portia labiata	64	53	3	5
Tauala lepidus	13	77	40	46
Trite auricoma	38	53	25	18
Trite planiceps	43	72	43	63
Zenodorus orbiculatus	2	50	100	0
Tests in tubes using house flies as prey				
Cheiracanthium stratioticum[1]	13	85	90	85
Clubiona cambridgei[1]	54	93	89	83
Dysdera crocata[1]	15	100	85	87
Supunna picta[1]	18	100	88	89
Bavia aericeps	15	100	7	13
Corythalia canosa	17	94	38	29
Cosmophasis sp.	16	88	14	38
Epeus sp. 2	7	100	0	57
Eris marginata	5	100	0	0
Euophrys parvula	22	95	43	82
Helpis minitabunda	50	100	6	34
Holoplatys planissima	12	92	20	25
Jacksonoides queenslandicus	16	94	7	0
Lyssomanes viridis	42	98	3	14
Marpissa marina	32	94	50	56
Mogrus dumicola	26	96	28	46
Mopsus mormon	10	80	0	40
Phidippus sp. 1	14	100	38	100
Phidippus sp. 2	9	100	13	89
Portia africana	7	86	17	57
Portia fimbriata	26	100	0	12
Portia labiata	24	83	11	33
Portia shultzi	10	100	20	50

Table 3.—Continued.

	n	Contact	Confront	Capture
Tauala lepidus	16	100	19	25
Trite auricoma	33	91	21	27
Trite planiceps	21	100	70	86
Tests in petri dishes using house flies as prey				
Clubiona cambridgei[1]	22	91	85	91
Dysdera crocata[1]	12	100	67	83
Supunna picta[1]	16	94	87	94
Bavia aericeps	15	93	0	0
Corythalia canosa	15	87	0	7
Cosmophasis sp.	14	86	8	0
Epeus sp.	9	89	0	11
Euophrys parvula	46	85	0	0
Helpis minitabunda	39	95	5	3
Holoplatys planissima	4	100	0	0
Jacksonoides queenslandicus	20	85	0	0
Lyssomanes viridis	35	94	0	9
Marpissa marina	26	100	4	4
Mopsus mormon	12	83	0	0
Portia africana	5	100	0	0
Portia labiata	66	89	0	0
Portia shultzi	10	100	0	0
Tauala lepidus	12	83	20	17
Trite auricoma	36	92	9	3
Trite planiceps	70	90	44	53

Prey-capture behavior in the absence of visual cues.—Salticids always lunged to catch prey, and were never observed to leap onto prey as they commonly do in light. No spider, salticid or non-salticid, ever lunged at the flies prior to being touched. *Cheiracanthium stratioticum* and *Clubiona cambridgei,* non-salticids, sometimes chased after flies that moved away following contact, but no salticid ever did this.

After lunging at flies, salticids sometimes held the flies for 1–5 sec with their fangs whilst appearing to make little or no attempt at using their legs to grasp the fly. In these instances, flies broke free or were released by the spiders but always stopped moving within 10 min of being bitten. During tests using sighted spiders in tubes, the following salticids made bite-then-release attacks on house flies: *Bavia aericeps* (1 of 2 captures recorded), *Corythalia canosa* (1 of 5), *Helpis minitabunda* (1 of 17), *Mogrus dumicola* (2 of 12), *Mopsus mormon* (1 of 4), *Phidippus* sp. 1 (2 of 14), *Portia labiata* (1 of 8), *Trite auricoma* (3 of 9) and *Trite planiceps* (2 of 18). After these attacks, spiders usually later

picked up the immobilized fly and ate it, the only exception being *Bavia aericeps*. *Trite planiceps* was the only salticid observed to kill a fruit fly by a bite-then-release attack (3 of 27). During tests in petri-dish arenas using house flies as prey, spiders that grasped flies always held onto them until they died.

DISCUSSION

Salticids are conventionally thought of as strictly diurnal hunters that shelter overnight, and this general impression is supported by observations of spider activity patterns in nature and in the laboratory (e.g., Jackson 1976; Givens 1978; Taylor 1997). Nonetheless, the present study finds that, as well as being extraordinarily adept visual predators (Forster 1977, 1979; Jackson & Pollard 1996; Bear & Hasson 1997), salticids are able to coordinate attacks using other senses when visual cues are unavailable. This finding in a laboratory context establishes a need for research investigating naturally occurring situations during which salticids might depend primarily or solely on cues other than vision to coordinate attacks.

Table 4.—Number of spiders that caught flies in light *vs.* dark. Species marked with a superscript 1 are non-salticids. Only columns 'Light only' and 'Dark only' are relevant for McNemar tests for significance of changes (Sokal & Rohlf 1981).

	Light only	Dark only	Both	Neither	McNemar test
Tests using fruit flies					
Clubiona cambridgei[1]	2	3	10	3	NS
Asemonea tenuipes	7	0	2	1	$P < 0.01$
Bavia aericeps	15	0	1	2	$P < 0.001$
Corythalia canosa	10	0	1	4	$P < 0.005$
Cosmophasis micarioides	14	0	2	3	$P < 0.001$
Cosmophasis bitaeniata	5	0	2	4	$P < 0.05$
Cyrba ocellata	6	0	1	3	$P < 0.025$
Euophrys parvula	17	0	3	5	$P < 0.001$
Epeus sp. 2	18	0	1	2	$P < 0.001$
Eris marginata	11	0	4	0	$P < 0.001$
Euryattus sp.	9	0	3	4	$P < 0.005$
Hasarius adansoni	13	1	3	3	$P < 0.005$
Helpis minitabunda	17	1	2	2	$P < 0.001$
Hentzia mitrata	5	0	2	1	$P < 0.05$
Holoplatys sp.	19	0	4	3	$P < 0.001$
Jacksonoides queenslandicus	20	0	4	4	$P < 0.001$
Lyssomanes viridis	15	0	0	4	$P < 0.001$
Marpissa marina	18	1	2	3	$P < 0.001$
Menemerus bivattatus	12	0	3	5	$P < 0.001$
Mopsus mormon	13	0	2	5	$P < 0.001$
Myrmarachne lupata	19	1	3	2	$P < 0.001$
Natta rufopicta	14	1	2	3	$P < 0.001$
Phidippus johnsoni	18	0	0	3	$P < 0.001$
Plexippus calcarata	17	0	3	1	$P < 0.001$
Portia labiata	9	2	0	11	$P < 0.05$
Simaetha paetula	19	0	3	1	$P < 0.001$
Tauala lepidus	12	1	3	1	$P < 0.005$
Thiania bhamoensis	22	1	2	2	$P < 0.001$
Thorellia ensifera	11	1	2	2	$P < 0.005$
Trite auricoma	19	0	6	1	$P < 0.001$
Trite planiceps	16	0	8	1	$P < 0.001$
Tularosa plumosa	5	0	2	2	$P < 0.05$
Viciria praemandibularis	13	0	3	4	$P < 0.001$
Zenodorus orbiculatus	15	0	1	3	$P < 0.001$
Tests using house flies					
Clubiona cambridgei[1]	0	2	5	1	NS
Bavia aericeps	8	0	2	0	$P < 0.005$
Euophrys parvula	5	0	2	1	$P < 0.05$
Helpis minitabunda	7	1	0	6	$P < 0.05$
Jacksonoides queenslandicus	8	0	1	1	$P < 0.005$
Marpissa marina	9	0	2	0	$P < 0.005$
Mopsus mormon	5	0	2	0	$P < 0.05$
Phidippus johnsoni	8	0	2	1	$P < 0.005$
Plexippus calcarata	6	0	1	1	$P < 0.025$
Tauala lepidus	5	0	2	0	$P < 0.05$
Trite auricoma	4	0	1	3	$P < 0.05$
Trite planiceps	8	0	4	0	$P < 0.005$

Acute vision is not a prerequisite for successful cursorial hunters. Many spiders from other families (i.e., non-salticids) are successful cursorial hunters despite lacking acute vision (e.g., Ctenidae, Pisauridae, Clubionidae, Gnaphosidae) and there is no obvious reason to presume that salticids could not also sometimes hunt cursorially when visual cues are not available. There is even anecdotal evidence that at least one salticid, *Phidippus otiosus* (Hentz 1846) [= *Phidippus pulcher* (Walckenaer 1837)], does sometimes hunt after nightfall (Reiskind 1982). Web-building spiders from other families lack acute vision, and instead use their webs as extensions of their tactile sense organs to hunt both during the day and at night (Witt 1975; Suter 1978; Jarman & Jackson 1986). Web-building salticids have at their disposal all of the prey-catching facilities used by web-builders from other families but whether salticids make use of these facilities when visual cues are absent is not known. Salticids that build webs (Jackson & Hallas 1986; Jackson & Pollard 1990) or web-like nests (Hallas & Jackson 1986a, b; Jackson & McNab 1989a) are prime candidates for investigation of nocturnal predation.

Although predation is conventionally envisaged as a means of gaining food, it may also function as defense (Curio 1976; Archer 1988). Salticids may commonly find themselves in situations that demand immediate responses to attacks in the absence of visual cues from the attacker. For example, salticids may be suddenly attacked by fast-moving predators in light (Jackson 1980; Young & Lockley 1987; Jackson & McNab 1989b; Jackson et al. 1990), in darkness when in their nests at night (Jackson 1976; Jackson & Griswold 1979; Jarman & Jackson 1986; Taylor 1997) or in dark places during the day. Additionally, salticids attacked in their nests during the day may be denied visual cues by the opaque walls of their nest (see Hallas & Jackson 1986b). How salticids mediate anti-predator behavior in these contexts has not yet been studied specifically, but immediate orientation and attack (similar to confrontation and 'immediate captures' in our experiments) might be an appropriate defense against an unidentified intruder.

The poorly known natural histories of most salticid species cause difficulty in interpreting the observed species differences in predation

success and aggressiveness toward flies in the absence of visual cues. Nonetheless, results of this laboratory study do suggest certain hypotheses about how salticids might respond in nature. For example, tendency to respond aggressively when touched by flies in darkness was not strongly associated with size, a measure of physical ability. Instead, we may consider each species' relationships with prey and enemies to understand why salticids varied in aggressiveness. Most likely, success in nature depends not only on a salticid's size or strength, but also on the types of predators and prey encountered and the situations in which encounters take place. For example, some large salticids may have responded timidly because their nocturnal predators are especially ferocious or encounters take place at sites where escape is easy, whereas some smaller salticids may have responded aggressively because their nocturnal intruders are less dangerous or because encounters with enemies in nature are difficult to escape.

Some salticids (e.g., *Euophrys parvula*, *Marpissa marina*), adjusted their tendency to confront and later catch flies in darkness depending on ease of avoidance. These species made greater use of the comparatively easy avoidance option when tested in expansive petri dishes, but they responded more aggressively when in tubes with few options for escape. If prey-capture was based on feeding considerations, then we would not have expected these differences. Instead, evasion of potential enemies, rather than hunting, seems a better explanation of non-visual predation by these salticids in our experiments.

Trite planiceps, the salticid for which non-visual predation was first reported by Forster (1982), appears to be a special case. Although other salticids often caught house flies when tested in tubes, *T. planiceps* was unusually aggressive and successful at prey-capture when tested in the more spacious petri-dishes. Perhaps, as was suggested by Forster (1982), *T. planiceps'* unusual aggressiveness is an adaptation related to frequent encounters with potential prey, dangerous intruders, or both in the restrictive dark recesses within rolled-up leaves where this species normally lives. *Trite planiceps* used in the present study share their habitat with each of the non-salticids tested. Of these, *Clubiona cambridgei, Cheiracanthium stratioticum* and *Taieria erebus* have

been observed eating *Trite planiceps* adults, juveniles and eggs in nature (PWT unpubl. data). Of course, other salticids tested also encounter enemies in darkness (Jackson 1976; Jarman & Jackson 1986), but the abundance of nocturnal hunting spiders and confining microhabitat inside rolled-up leaves may make encounters with predators unusually frequent and unusually difficult to escape.

ACKNOWLEDGMENTS

LITERATURE CITED

Archer, J. 1988. The Behavioural Biology of Aggression. Cambridge Univ. Press, Cambridge. 257 pp.

Bear, A. & O. Hasson. 1997. The predatory response of a stalking predator, *Plexippus paykulli,* to camouflage and prey type. Anim. Behav., 54: 993–998.

Blest, A.D., R.C. Hardie, P. McIntyre & D.S. Williams. 1981. The spectral sensitivities of identified receptors and the function of retinal tiering in the principal eyes of a jumping spider. J. Comp. Physiol., 145:227–239.

Blest, A.D., D.C. O'Carroll & M. Carter. 1990. Comparative ultrastructure of layer I receptor mosaics in principal eyes of jumping spiders: The evolution of regular arrays of light guides. Cell Tiss. Res., 262:445–460.

Clark, D.L. & G.W. Uetz. 1994. Sequence analysis of courtship behavior in the dimorphic jumping spider *Maevia inclemens* (Araneae, Salticidae). J. Arachnol., 22:94–107.

Coddington, J.A. & H.W. Levi. 1991. Systematics and evolution of spiders (Araneae). Ann. Rev. Ecol. Syst., 22:565–592.

Crane, J. 1949. Comparative biology of salticid spiders at Rancho Grande, Venezuela. Part IV. An analysis of display. Zoologica, 34:159–215.

Curio, E. 1976. The ethology of predation. Springer-Verlag, Berlin. 250 pp.

Dill, L.M. 1974. Predatory behaviour of the zebra spider, *Salticus scenicus* (Araneae, Salticidae). Canadian J. Zool., 53:1284–1289.

Drees, O. 1952. Untersuchungen über die angeboren en Verhaltensweisen bei Springspinnen (Salticidae). Z. Tierpsychol., 9:169–207.

Forster, L.M. 1977. A qualitative analysis of hunting behaviour in jumping spiders (Araneae: Salticidae). New Zealand J. Zool., 4:51–62.

Forster, L.M. 1979. Visual mechanisms of hunting behaviour in *Trite planiceps,* a jumping spider (Araneae: Salticidae). New Zealand J. Zool., 6: 79–93.

Forster, L.M. 1982. Non-visual prey-capture in *Trite planiceps,* a jumping spider (Araneae, Salticidae). J. Arachnol., 10:179–183.

Freed, A.N. 1984. Foraging behaviour in the jumping spider *Phidippus audax*: bases for selectivity. J. Zool., London, 203:49–61.

Givens, R.P. 1978. Dimorphic foraging strategies of a salticid spider (*Phidippus audax*). Ecology, 59:309–321.

Hallas, S.E.A. & R.R. Jackson. 1986a. A comparative study of Old and New World lyssomanines(Araneae, Salticidae): Utilisation of silk and predatory behaviour of *Asemonea tenuipes* and *Lyssomanes viridis*. New Zealand J. Zool., 13: 543–551.

Hallas, S.E.A. & R.R. Jackson. 1986b. Prey-holding abilities of the nests and webs of jumping spiders (Araneae, Salticidae). J. Nat. Hist., 20: 881–894.

Heil, K.H. 1936. Beiträge zur Physiologie und Psychologie der Springspinnen. Z. Vergl. Physiol., 23:125–149.

Hill, D.E. 1979. Orientation by jumping spiders of the genus *Phidippus* (Araneae, Salticidae) during the pursuit of prey. Behav. Ecol. Sociobiol., 5: 301–322.

Jackson, R.R. 1976. Predation as a factor in the mating strategy of the jumping spider *Phidippus johnsoni* (Salticidae, Araneae). Psyche, 83:243–255.

Jackson, R.R. 1977. Courtship versatility in the jumping spider, *Phidippus johnsoni* (Araneae: Salticidae). Anim. Behav., 25:953–957.

Jackson, R.R. 1980. Cannibalism as a factor in the mating strategy of the jumping spider *Phidippus johnsoni* (Araneae, Salticidae). Bull. British Arachnol. Soc., 5:129–133.

Jackson R.R. & C.E. Griswold. 1979. Nest associates of *Phidippus johnsoni* (Araneae, Salticidae). J. Arachnol., 7:59–67.

Jackson, R.R. & S.E.A. Hallas. 1986. Comparative biology of *Portia africana, P. albimana, P. fimbriata, P. labiata,* and *P. shultzi,* araneophagic, web-building jumping spiders (Araneae: Salticidae): Utilization of webs, predatory versatility, and intraspecific interactions. New Zealand J. Zool., 13:423–489.

Jackson, R.R. & A.M. McNab. 1989a. Display, mating, and predatory behaviour of the jumping

spider *Plexippus paykulli* (Araneae: Salticidae). New Zealand J. Zool., 16:151–168.

Jackson, R.R. & A.M. McNab. 1989b. Display behaviour of *Corythalia canosa,* an ant-eating jumping spider (Araneae: Salticidae) from Florida. New Zealand J. Zool., 16:169–183.

Jackson, R.R. & S.D. Pollard. 1990. Web-building and predatory behaviour of *Spartaeus spinimanus* and *Spartaeus thailandicus,* primitive jumping spiders (Araneae, Salticidae) from South-east Asia. J. Zool., London, 220:561–567.

Jackson, R.R. & S.D. Pollard. 1996. Predatory behavior of jumping spiders. Ann. Rev. Entomol., 41:287–308.

Jackson, R.R., S.D. Pollard, A.M. McNab & K.J. Cooper. 1990. The complex communicatory behaviour of *Marpissa marina,* a New Zealand jumping spider (Araneae: Salticidae). New Zealand J. Zool., 17:25–38.

Jackson, R.R., P.W. Taylor, A.S. McGill & S.D. Pollard. 1995. The web and prey-capture behaviour of *Diaea* sp., a crab spider (Thomisidae) from New Zealand. Rec. Western Australian Mus., 52: 33–37.

Jackson, R.R. & A. Van Olphen. 1991. Prey-capture techniques and prey preferences of *Corythalia canosa* and *Pystira orbiculata,* ant-eating jumping spiders (Araneae, Salticidae). J. Zool., London, 223:577–591.

Jarman, E.A.R. & R.R. Jackson. 1986. The biology of *Taieria erebus* (Araneae, Gnaphosidae), an araneophagic spider from New Zealand: silk utilization and predatory versatility. New Zealand J. Zool., 13:521–541.

Land, M.F. 1985. The morphology and optics of spider eyes. Pp. 53–78. *In* Neurobiology of Arachnids. (F.G. Barth, ed.), Springer-Verlag, Berlin.

Li, D. & R.R. Jackson. 1996. Prey preferences of *Portia fimbriata,* an araneophagic, web-building jumping spider (Araneae: Salticidae) from Queensland. J. Insect Behav., 9:613–642.

Li, D., R.R. Jackson & A. Barrion. 1997. Prey preferences of *Portia labiata, P. africana,* and *P.*

shultzi, araneophagic jumping spiders (Araneae: Salticidae) from the Philippines, Sri Lanka, Kenya and Uganda. New Zealand J. Zool., 24:333–349.

Peaslee, A.G. & G. Wilson. 1989. Spectral sensitivity in jumping spiders (Araneae, Salticidae). J. Comp. Physiol. A, 164:359–363.

Reiskind, J. 1982. Observations of night activity in *Phidippus otiosus* (Hentz). Peckhamia, 2:40.

Snelling, R.R. 1983. Prey-stalking behavior of a thomisid spider, *Xysticus californicus* Keyserling (Araneae, Thomisidae). Entomol. News, 94:201–203.

Sokal, R.R. & F.J. Rohlf. 1981. Biometry. Freeman: San Francisco. 859 pp.

Stratton, G.E. 1984. Behavioural studies of wolf spiders: A review of recent studies. Rev. Arachnol., 6:57–70.

Suter, R.B. 1978. *Cyclosa turbinata* (Araneae, Araneidae): Prey discrimination via web-borne vibrations. Behav. Ecol. Sociobiol., 3:283–296.

Tarsitano, M.S. & R.R. Jackson. 1997. Araneophagic jumping spiders discriminate between detour routes that do and do not lead to prey. Anim. Behav., 53:257–266.

Taylor, P.W. 1995. Jumping spiders alternate turns in the absence of visual cues. Int. J. Comp. Psychol., 8:69–76.

Taylor, P.W. 1997. Brood-defense as a function of maternal brood-attendance in *Trite planiceps* (Araneae, Salticidae). Bull. British Arachnol. Soc., 10:341–343.

Witt, P.N. 1975. The web as a means of communication. Biosc. Comm., 1:7–23.

Yamashita, S. 1985. Photoreceptor cells in the spider eye: Spectral sensitivity and efferent control. Pp. 103–117. *In* Neurobiology of Arachnids. (F.G. Barth, ed.), Springer-Verlag, Berlin.

Young, O.P. & T.C. Lockley. 1987. Dragonfly predation upon *Phidippus audax* (Araneae, Salticidae). J. Arachnol., 16:121–122.

RESEARCH NOTE

A NEW METHOD OF MARKING SPIDERS

Marking spiders for future identification is essential for many types of ecological and behavioral studies. The perfect marker would not be lost, become unrecognizable, or be transferred to unmarked individuals during the time-frame of the study. The marker, or its application procedure, should not affect health, survivability, or behavior of the individual—including their mobility and catchability. In addition, a simple, rapid protocol with minimal handling is desirable.

However, marking spiders is difficult. A dab of paint applied externally is used commonly, but spiders have little area to paint: the prosoma bears the eyes, the opisthosoma is very flexible, and the joints in legs may seize if an excessive amount of paint is applied. The process usually requires direct handling of the animal, which can be damaging for fragile species without strongly sclerotized exoskeletons. Furthermore, such an external mark will only persist until the exoskeleton is molted.

Histological stains, as a form of internal marking, are an alternative to paints. Several of these have been used in insects (Zacharuk 1963; Barbosa & Peters 1971; Lai et al. 1983; Su et al. 1988, 1991; Oi & Su 1994), and we thought it likely that stains could also be used in spiders. The lightly sclerotized exoskeleton of the opisthosoma in some species could be advantageous as internal staining should be seen more clearly. Further, internal markers should persist between molts. We wanted a simple staining technique that avoided handling the spiders, so we capitalized on their predacious nature and offered them stained prey.

We used termites as the prey and chose to test two non-toxic, fat stains that are suitable as markers in termites, Nile Blue A and Sudan Yellow (Fast Garnet). Two species of termite were used, *Coptotermes lacteus* (Froggatt 1898) were stained blue (0.5% Nile Blue A in distilled water), whereas *Nasutitermes exitio-*sus (Hill 1925) were stained pink (4.0% Sudan Yellow dissolved in acetone) (see Evans 1997 for details). The termites were fed stained filter paper for six days, by which time they were colored deeply.

We used *Pholcus phalangioides* (Fuesslin 1775) (Pholcidae) as a test species because of its fragile morphology, translucent exoskeleton and ubiquity. We collected 49 *P. phalangioides* of varying instars from the CSIRO Black Mountain site in Canberra. They were weighed and placed in plastic containers (20 × 15 cm), kept at 28 °C and 90% humidity, sprayed with water, and allowed to weave a web. The spiders were assigned to one of three treatments: blue (i.e., fed blue *C. lacteus*), yellow (i.e., fed pink *N. exitiosus*), and control (i.e., fed unstained *C. lacteus* and *N. exitiosus*). There were no significance differences in initial weight between treatments ($F2, 46 = 1.289, P > 0.2$) (Table 1).

After two days, spiders in the two stain treatments were fed 2–5 stained termites, depending on body weight (*ca.* 1 termite per 8 mg of spider body weight), whereas the control spiders were fed similar amounts of unstained termites. Color was clearly visible in the abdomens by the next day: 17 of the 22 spiders in the blue treatment, 8 of the 15 spiders in the yellow treatment. The unstained spiders in those treatments were then fed more stained termites on the second day, which colored them by the third day. The marking was not uniform over the opisthosoma; instead it was most obvious in lighter colored patches and on the ventral surface. This was particularly so in the yellow treatment. We changed the diet to unstained termites once spiders were colored. The spiders captured and ate all termites similarly; regardless of prey color, the termites were always captured and feeding began within five minutes of the termites being dropped into webs. The color in the spiders faded slowly and forwards: the anterior, ventral part of the abdomen remained pink for

Treatment	N	Initial Weight (mg)	Final Weight (mg)	Weight Change Ratio	Number of Molts
Control	12	19.54 ± 3.39	23.0 ± 2.77	1.30 ± 0.08	1.00 ± 0.25
Blue	22	14.94 ± 2.05	18.8 ± 1.78	1.41 ± 0.07	1.00 ± 0.15
Yellow	15	20.11 ± 2.94	23.3 ± 2.20	1.35 ± 0.10	0.67 ± 0.21

around one week (Sudan Yellow) or two weeks (Nile Blue A). Once the color had faded almost completely, we fed the spiders one or two stained termites, which re-colored the spiders.

The experiment concluded after the spiders had been colored and faded three times, over a period of five weeks. There were no deaths, and the spiders grew non-significantly differently during this time. Spiders molted *ca.* once on average in each treatment ($F_{2, 46} = 0.973$, $P > 0.3$), importantly the stain persisted between molts. Spiders had a similar final weight in each treatment ($F_{2, 46} = 1.554$, $P > 0.2$) and had similar growth in each treatment ($F_{2, 46} = 0.426$, $P > 0.6$) (Table 1). Of the eight adult females in the experiment, six were stained (three each blue and pink); and four produced an uncolored eggsac (three blue and one pink). These were carried in the females' chelicerae without any obvious deviation from normal behavior. We did not wait for the eggs to hatch, and so do not know if they were viable.

We concluded from this simple experiment that both histological stains tested in this study do have potential as markers for *P. phalangioides,* and perhaps for other spiders. Although neither marked the spiders permanently, the colors did persist for up to 21 days especially in younger instars at a constant 28 °C and could be reapplied. Importantly, neither stain appeared to affect the behavior or growth of the spiders: webs were destroyed when spiders were removed for weighing, all spiders in all treatments constructed new webs within a day, and weight changes were similar (Table 1). More elaborate laboratory and field trials are necessary to confirm these findings. Perhaps the best aspect of histological stain markers was the marking procedure. It was quick, simple and did not include handling the spiders, thus ensuring an absolute minimum of disturbance to the animal.

The stains tested in this study were not perfect markers as they faded, necessitating re-marking. However, remarking was simple and did not appear to affect the spider. Although no spiders died in this study, long term effects may arise from stains applied early in the life cycle (see discussion in Barbosa & Peters 1971 for effects on some insects). Field studies need to address changes in mortality due to predation (e.g., marked individuals may be either attractive or repulsive for their predators). It is also possible that the stains could be transmitted to unmarked spiders, if they successfully invaded the web of and ate the marked individual.

There are other histological stains which have potential as markers. We have also fed *C. lacteus* stained with Neutral Red (0.5% in water) to 12 *P. phalangioides* (mean weight 26.8 g). This colored the spiders purple overnight, with similar variation in the opisthosoma to that described above, persisting for two weeks without apparent harm. Other stains used on termites include Sudan Red 4, Sudan Red 7B and Sudan Black (Su et al. 1988; 1991; see also Conn 1977 for general histological stain information). Other insect species have been marked using histological stains (e.g., beetle larvae, Zacharuk 1963) so these could be used instead of termites as prey. Of course this method of internal marking will only mark those spider species that do not have strong coloring in their exoskeletons. Yet it may be possible to mark lightly colored spiderlings of such species. We hope that other workers can adapt this technique to their species and studies, but after careful assessment of the limitations found or suggested from this study.

LITERATURE CITED

Barbosa, P. & T.M. Peters. 1971. The effects of vital dyes on living organisms with special ref-

erence to methylene blue and neutral red. His-
tochem. J., 3:71–93.

Conn, H. 1977. Biological Stains: A Handbook On
The Nature And Uses Of The Dyes Employed In
The Biological Laboratory (9th ed). Williams &
Wilkins, Baltimore.

Evans, T.A. 1997. Evaluation of marks for Austra-
lian subterranean termites (Isoptera: Rhinoter-
mitidae and Termitidae). Sociobiology, 29:1–16.

Lai, P.Y., M. Tamashiro, J.K. Fujii, J.R. Yates &
N.Y. Su. 1983. Sudan red 7B, a dye marker for
Coptotermes formosanus. Proc. Hawaiian Ento-
mol. Soc., 24:277–282.

Oi, F.M. & N.Y. Su. 1994. Stains tested for mark-
ing *Reticulitermes flavipes* and *R. virginicus*
(Isoptera: Rhinotermitidae). Sociobiology, 24:
241–268.

Su, N.Y., R.H. Scheffrahn & P.M. Ban. 1988. Re-
tention time and toxicity of a dye marker, Sudan
red 7B, on Formosan and eastern subterranean
termites (Isoptera: Rhinotermitidae). J. Entomol.
Science, 23:235–239.

Su, N.Y., P.M. Ban & R.H. Scheffrahn. 1991. Eval-
uation of twelve dye markers for population
studies of the eastern and Formosan subterranean
termite (Isoptera: Rhinotermitidae). Sociobiolo-
gy, 19:349–362.

Zacharuk, R.Y. 1963. Vital dyes for living elaterid
larvae. Canadian J. Zool., 41:991–996.

Theodore A. Evans and **Patrick V. Gleeson:**
CSIRO Division of Entomology, Canberra,
ACT 2601, Australia

RESEARCH NOTE

A DESCRIPTION OF AN UNUSUAL DOME WEB OCCUPIED BY EGG-CARRYING *HOLOCNEMUS PLUCHEI* (ARANEAE, PHOLCIDAE)

Spiders use silk to construct prey-capture webs, protective tubes and retreats, and egg sacs (reviewed in Nentwig & Heimer 1987). *Holocnemus pluchei* (Scopoli 1763) build irregular, often curved prey-capture sheets, and, like other pholcids, hold their eggs in a loose bundle in their chelicerae. Egg-carrying *H. pluchei* are found inside unusual dome-shaped webs that are easily distinguishable from the normal prey-capture web. Dome webs are generally spherical, completely surrounding the female and her eggs, and attached to structures such as buildings or the stiff inner branches of bushes. After the eggs hatch, the female leaves the dome. Spiderlings remain in the dome until their first molt. After molting, they disperse and either construct a sheet web or join the webs of other spiders, where they live together on the same sheet (Jakob 1991; unpubl. data). Here we describe dome webs in the field, including the presence of associated spiders outside of the domes, and the responses of spiders in-and-near dome webs to the vibration of a tuning fork, which generally elicits a prey-capture response from *H. pluchei* spiders on prey-capture sheets (Jakob 1991).

H. pluchei spiders are abundant in the Central Valley of California, and are commonly found in bushes, especially junipers (*Juniperus* sp.), and around human habitation. Although domes can be found deep within juniper bushes, that location makes them difficult to study. Therefore, we focused on dome webs found under an overhanging outdoor ceiling, approximately 2 m high, of Briggs Hall at the University of California at Davis. Observations were made on 16 and 17 August 1995.

We selected 24 dome webs for study. Nineteen contained a female with an egg sac in her chelicerae and five held a female surrounded by recent hatchlings (first instar spiderlings).

Each web was numbered with masking tape adjacent to the web. Dome diameters were measured with a 10 cm ruler. Activity of females in the domes and of associated spiders was noted before and after the application of a tuning fork to the web. Behavior patterns noted were: approaching or wrapping the tuning fork, considered to be predatory behaviors; bouncing, a rapid up-and-down movement which has been shown to be an anti-predator response (Jackson et al. 1993); or no response. Webs were revisited the next day.

Domes averaged 5.04 cm in diameter (SE = 1.33) (Fig. 1). Nineteen were on the ceiling and five were in the corner formed by the ceiling and the wall. Fifteen were complete domes with no damage; nine had small holes in the side. Domes were composed of fine silken strands, with no apparent pattern in their arrangement. Strands were occasionally clumped into small balls on the surface of the dome. We saw no viscid balls, as has been noted in another pholcid (Briceño 1985).

There was at least one conspecific within 15 cm of 71% of females in web domes. These associated spiders were not on prey-capture webs, but were either resting directly on the outside of the dome, on a few silk threads attached to the building, or on the concrete overhang to which the dome was attached. The nearest groups of prey-capture webs were on bushes at least 10 m away from the domes described here. We have never seen spiders associated in the same way with the sheet webs used in prey capture; spiders near sheet webs are either in a web themselves or are moving rapidly through the vegetation. We identified classified spiders as mature males, mature females, medium juveniles (probably 4th instar) and small juveniles (2nd or 3rd instar) (representative measurements of size classes are given in Jakob 1994). The most common associ-
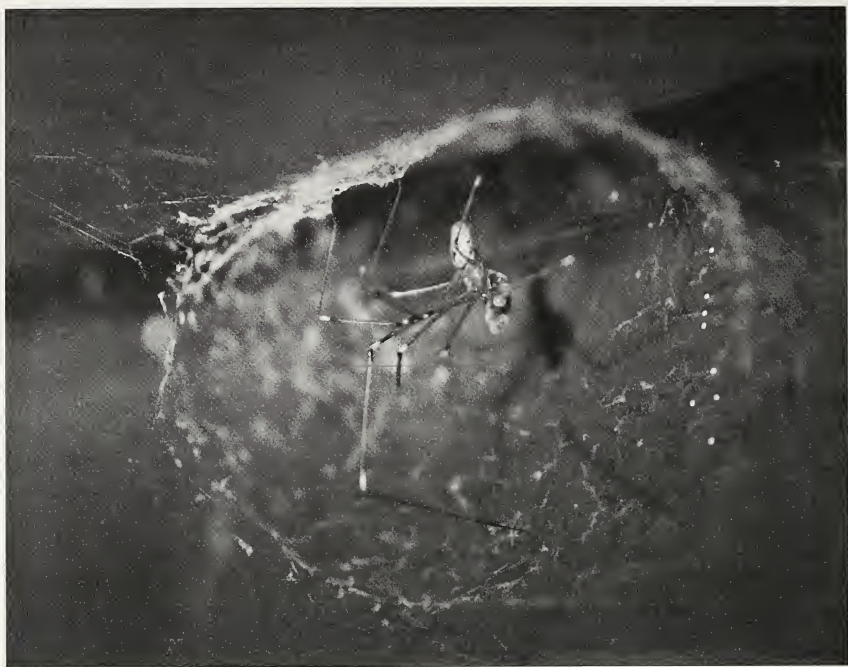
Figure 1.—Female *Holocnemus pluchei* and eggs, surrounding by a dome web.

ates were males (Table 1). On day 1, most females with eggs were accompanied by at least one male (14 of 19), but only one female with hatchlings was accompanied by a male; this difference nears statistical significance (contingency test, $\chi^2 = 3.818$, $df = 1$, $P = 0.0507$). On the second day, 11 of 19 females with eggs were accompanied by at least one male. Only three females with hatchlings were located on day 2, and one was accompanied by a male; this did not differ significantly from females with eggs.

We compared spiders that were inside domes, associated with domes, and on prey-capture webs. The data on spiders from prey-capture webs came from a survey conducted in July 1996 (Johnson 1997; Johnson & Jakob in press). In that survey, the number and class (small juvenile, medium juvenile, adult female, adult male, and female with eggs or

Table 1.—Spiders within 15 cm of the domes of focal females on consecutive days.

	Day 1	Day 2
Females with eggs		
1 male	8	8
2 males	2	
1 male and 1 female with eggs	2	1
1 male and 1 female with new hatch	1	1
1 female, 1 male, 1 medium, and 2 small		1
1 small	3	2
None	3	6
Total webs with eggs	19	19
Females with hatchlings		
1 male and 1 female	1	
1 male, 1 female, and 1 small		1
None	4	2
Total webs with hatchlings	5	3

Table 2.—A comparison of the number of spiders in different sex and age categories that were on prey-capture (sheet) webs, those that were inside domes, and those that were associated with domes on day 1. Expected values are in parentheses. Differences are significant ($\chi^2 = 2173.8$, $df = 8$, $P < 0.0001$). Patterns for day 2 are similar ($\chi^2 = 2117.3$, $df = 8$, $P < 0.0001$). [1]Data from Johnson 1997; Johnson & Jakob in press.

	Sheet webs[1]	Inside domes	Associated with domes
Females with eggs or hatchlings	0 (23.4)	24 (0.3)	0 (0.3)
Females	657 (645.7)	0 (7.8)	4 (7.5)
Males	123 (135.8)	0 (1.6)	16 (1.6)
Medium juveniles	763 (745.3)	0 (9.0)	0 (8.6)
Small juveniles	439 (431.8)	0 (5.2)	3 (5.0)

hatchlings) of all spiders on 1406 webs were recorded. Methods followed Jakob (1991), and included touching a ringing tuning fork to the web to attract spiders that might be hidden by vegetation at the web edge.

We found significant differences in the classes of spiders that were most likely to be found on prey-capture webs, inside domes, or associated with domes (Table 2). Dome webs contained more females with eggs or hatchlings than expected. Associates of domes were significantly more likely to be adult males than expected. As a follow-up test, we also compared dome associates only to spiders on prey-capture sheets, omitting females with eggs or hatchlings. Again, we found a significantly greater proportion of males associated with domes than on prey-capture webs (day 1: $\chi^2 = 143.1$, $df = 3$, $P < 0.0001$; day 2: $\chi^2 = 92.3$, $df = 3$, $P < 0.0001$).

Females with eggs and females with hatchlings behaved differently in response to the tuning fork ($\chi^2 = 18.24$, $df = 1$, $P < 0.0001$, Table 3). Females with eggs never exhibited predatory behavior, but instead gave no re-sponse or bounced. Four of five females with hatchlings attempted to wrap the tuning fork tip. These data suggest that the prey-capture response of the females is suppressed while she is holding eggs in her chelicerae, but returns when the eggs have hatched. Associated male and juvenile spiders also frequently attacked the tuning fork (Table 3).

Our data suggest that male spiders may be attracted to females in dome webs, particularly females carrying egg sacs. It is not known whether males are seeking to capture prey by using the dome web, seeking protection from predators by associating with females in domes, or seeking to copulate with the females. The first possibility seems unlikely as we never saw prey in these small webs. The second possibility is difficult to evaluate, given the lack of evidence of predation in this population. It seems most likely that males are seeking copulations with females: *H. pluchei* exhibits last-male sperm priority (Kaster & Jakob 1997), so a female that has already been mated would still be valuable to a male. It is not clear why juvenile or female spiders are

Table 3.—Responses of focal spiders in dome webs ($n = 24$) and associated spiders outside of dome ($n = 23$) webs to a ringing tuning fork.

	No response or slight movement	Bounce	Approach tuning fork	Wrap tuning fork
Focal female with eggs	15	4		
Focal female with hatchlings		1		4
Associated male	2	6	4	4
Associated female	1			
Associated female with eggs	1	1		
Associated female with hatchlings	1			
Juvenile			3	

found near domes and not on prey-capture webs. Our data from two consecutive days suggests that movements of associated spiders are not uncommon.

To our knowledge, special webs that surround the female and her egg case have not been previously described, although special webs built for spiderlings are known. Females of several species in the Pisauridae carry their egg until it hatches, build a special "nursery-web" for the spiderlings, and then guard them (reviews in D'Andrea 1987, Buskirk 1982). Feeding by the female is suppressed during guarding (Rabaud 1936, cited in D'Andrea 1987). Similar webs and guarding behavior have been reported in the Oxyopidae (Gertsch 1979).

Two functions of the dome web are likely. First, the dome web serves as a place from which spiderlings may hang during molting. In the laboratory, first-instar spiderlings removed from their dome webs and housed alone do not produce a web and subsequently die during their first molt. A second function that may have more bearing on the unusual shape of the web is an anti-predator function: by surrounding herself and her brood with silk, females may be able to sense vibrations of approaching predators more readily. Protection from predators is one of the proposed functions of maternal guarding in spiders (reviewed in Fink 1987), and guarding has been shown to significantly reduce predation on egg sacs in the green lynx spider (Fink 1986, 1987; Willey & Adler 1989). At this time, we are unable to assess this hypothesis for *H. pluchei* because the severity of interspecific predation pressure in either California or in its native habitat is not known. However, cannibalism is quite common in the California populations (EMJ pers. obs.), and it is possible that dome webs function to reduce cannibalism on hatchlings.

LITERATURE CITED

Briceño, R. 1985. Sticky balls in webs of the spider *Modisimus* sp. (Araneae, Pholcidae). J. Arachnol., 13:267–269.

Buskirk, R.E. 1982. Sociality in the Arachnida. Pp. 282–367. *In* Social Insects, Vol. II. (H.R. Hermann, ed.). Academic Press, New York.

D'Andrea, M. 1987. Social behaviour in spiders (Arachnida, Aranea). Italian J. Zool., Monogr. 3.

Fink, L.S. 1986. Costs and benefits of maternal behaviour in the green lynx spider (Oxyopidae, *Peucetia viridans*). Anim. Behav., 34:1051–1060.

Fink, L.S. 1987. Green lynx spider egg sacs: sources of mortality and the function of female guarding (Araneae, Oxyopidae). J. Arachnol., 15:231–239.

Gertsch, W.J. 1979. American Spiders. Van Nostrand Reinhold Company, New York.

Jackson, R.R., E.M. Jakob, M.B. Willey & G.E. Campbell. 1993. Anti-predator defences of a web-building spider, *Holocnemus pluchei* (Araneae, Pholcidae). J. Zool. London, 229:347–352.

Jakob, E.M. 1991. Costs and benefits of group living for pholcid spiderlings: Losing food, saving silk. Anim. Behav., 41:711–722.

Jakob, E.M. 1994. Contests over prey by group-living pholcids (*Holocnemus pluchei*). J. Arachnol., 22:39–45.

Johnson, S.A. 1997. Leg loss in male *Holocnemus pluchei*: What are the costs? Master's thesis, Bowling Green State University.

Johnson, S.A. & E. Jakob. In press. Leg loss in a spider has minimal costs in competitive ability and development. Anim. Behav.

Kaster, J. & E.M. Jakob. 1997. Last-male sperm priority in a haplogyne spider: Correlations between female morphology and patterns of sperm usage. Ann. Entomol. Soc. America, 90:254–259.

Nentwig, W. & S. Heimer. 1987. Ecological aspects of spider webs. Pp. 211–225. *In* Ecophysiology of Spiders. (W. Nentwig, ed.). Springer-Verlag, Berlin.

Rabaud, E. 1936. Notes sur le comportement maternel de *Pisaura mirabilis*. Livre jubil. Bouvier, Paris, 93–96.

Willey, M.B. & P.H. Adler. 1989. Biology of *Peucetia viridans* (Araneae, Oxyopidae) in South Carolina, with special reference to predation and maternal care. J. Arachnol., 17:275–284.

Kris A. Sedey and **Elizabeth M. Jakob**[1]: Department of Biological Sciences, Bowling Green State University, Bowling Green, Ohio 43403 USA

[1] Current address: Department of Entomology, University of Massachusetts, Amherst, Massachusetts 01003 USA.

RESEARCH NOTE

MULTI-SPECIES AGGREGATIONS IN NEOTROPICAL HARVESTMEN (OPILIONES, GONYLEPTIDAE)

Harvestmen are generally vagile and solitary but some species may be found in stationary aggregations. Gregariousness in harvestmen has been recorded in some Palpatores (Cockerill 1988 and incl. ref.; Coddington et al. 1990; Holmberg et al. 1984) and Laniatores species (Capocasale & Bruno-Trezza 1964; Acosta et al. 1993; Pinto-da-Rocha 1993). Multi-species aggregations have been reported once for three Leiobuninae species (Palpatores) in the southern USA (Cockerill 1988).

On 3 and 16 November 1996, multi-species aggregations of harvestmen were found in the low vegetation in a swampy area of Serra do Cipó (19°17′S, 43°35′W, 1200 m elevation), Minas Gerais State, Brazil. The local vegetation consists of Montane Fields ("campo rupestre"): mainly shrubs and low herbs growing in thin and rocky soil. Water infiltration into the ground was retarded by the layers below the thin soil. As a result, with any minor rainfall, the whole area became a swamp (Joly 1970). We sampled a 460 m² plot in a swamp in the early afternoon. All harvestmen found were collected and immediately preserved in 70% ethanol. During the survey we also observed the behavioral responses of the individuals to disturbance (such as attempts to escape, immobility, discharge of odorous secretions). Voucher specimens were deposited in the arachnological collection of the Museu de Zoologia da Universidade de São Paulo (MZUSP).

Harvestmen were found either in clumps of roots of gramineous species, or partially buried in the mud below these clumps. The soil in the basal portion of clumps was still muddy but not saturated to the point that pools of water were still present. We found 93 individuals belonging to three species of the family Gonyleptidae: *Despirus montanus* Mello-Leitão 1941 (subfamily Mitobatinae), *Eugyndes* sp. (a new species of the subfamily Pachyli-

nae) and *Holoversia nigra* Mello-Leitão 1940 (subfamily Gonyleptinae). Nine individuals (9.7%) were found isolated, not associated with any aggregation: four *D. montanus* (1♂3♀), three *Eugyndes* sp. (1♂2♀) and two *H. nigra* (1♂1♀). The remaining 84 individuals (90.7%) were found in five multi-species aggregations. The average number of individuals per cluster was 16.8 (SD = 11.1; range 5–34; n = 5). *Despirus montanus* and *Eugyndes* sp. were the most commonly encountered species in the aggregations since 95.2% of the individuals in all aggregates belonged to these species (Table 1). In both species, the sex ratio was not significantly different from 1:1 (*D. montanus* — χ^2 = 2.38; *Eugyndes* sp. — χ^2 = 1.68; df = 1; P > 0.05). *Holoversia nigra* was present in three aggregations and represented by only a few individuals—generally one or two per aggregation. The two isolated individuals of this species were found in the swamp area at distances of 1 and 2 m from the nearest aggregation where this species was not found. Table 1 shows the occurrence of species within aggregates.

When the aggregated individuals were disturbed, it appeared that only *H. nigra* released repugnatory substances. After the discharge, the individuals of this species abandoned the aggregations slowly. Disturbed individuals of *D. montanus* and *Eugyndes* sp. fled the place of disturbance or hid themselves in the base of the root clumps. Even when these species were manipulated they did not release detectable defensive secretions. Some laniatorid species use their repugnatory substances very sparingly, if at all (see Cokendolpher 1987; Roach et al. 1980).

Even though the water had receded at least one night before the harvestmen were found, they were still aggregated. Thus we reject the hypothesis that the harvestmen had aggregated in the root clumps to avoid drowning and had not had time to disperse. Gregarious be-

Table 1.—Species occurrence within five different multi-species aggregations of 84 harvestmen in a swamp in Serra do Cipó, Minas Gerais State, Brazil.

Holoversia nigra		Eugyndes sp.		Despirus montanus		Total # of individuals
Male	Female	Male	Female	Male	Female	
0	1	1	1	1	1	5
1	0	1	1	3	4	10
0	0	6	3	1	5	15
1	1	8	6	2	2	20
0	0	7	4	9	14	34
4.8%		45.2%		50.0%		84

havior in harvestmen has been interpreted in several ways according to Holmberg et al. 1984. The first interpretation is that the aggregations are formed in optimal places in order to avoid dehydration and exposure to light. The risk of dehydration must be low in the basal portion of the gramineous clump, since this microhabitat is constantly moist. Besides, all swamp area was under similar light conditions and the aggregation places were not patches of darkened areas. Thus the microhabitat explanation is not adequate to explain why the aggregations are formed in very different locations in the swamp. We can not reject the hypothesis, however, that multi-species aggregations are formed in more protected areas (due to greater interpenetration of the grass roots, for example) and thereby serve as hiding places from predators.

Another hypothesis is that the gregarious behavior increases the defensive ability against predators by the collective action of the repulsive substances secreted by these animals. This hypothesis may be supported by the fact that disturbance of an aggregate is immediately followed by a discharge of a substance with a strong, sour smell, produced by at least one species of harvestmen. Thus the multi-species aggregations of harvestmen may rely on the fact that the non-chemically protected species (i.e., those species which rarely released these chemicals: *D. montanus* and *Eugyndes* sp.) may get protection from aggregating with chemically-protected species (*H. nigra*). On the other hand, harvestmen that secrete noxious chemicals may gain benefit from the presence of non-secreting harvestmen, by the dilution effect (*sensu* Krebs & Davies 1993; see also Calvert et al. 1979; Duncan & Vigne 1979; Foster & Treherne

1981). By living in groups, the chemically-protected species may diminish the risk of being preyed upon because there are more chances that another individual be the victim. Although *H. nigra* was not found in all clusters, it is possible that it was present in the formation of the aggregation. Both *D. montanus* and *Eugyndes* sp. showed a tendency to aggregate, and individuals found isolated may temporarily have moved away from aggregations or have been expelled by other individuals of the group. Capocasale & Bruno-Trezza (1964) suggested that the expulsion of conspecifics from clusters was the reason why isolated individuals were found in *Acanthopachylus aculeatus* (Kirby 1818), but the reasons for this were not stated in that work.

Even if mating groups could be one of the reasons to the formation of mono-species aggregations (Holmberg et al. 1984), other effects like dilution and chemical protection could result in the incorporation of additional species to this groups. In the future, experimental studies should be performed in order to understand the evolutionary significance of gregarious behavior in harvestman.

ACKNOWLEDGMENTS

LITERATURE CITED

Acosta, L.E., T.I. Poretti & P.E. Mascarelli. 1993. The defensive secretions of *Pachyloidellus goliath* (Opiliones, Laniatores, Gonyleptidae). Bonn. Zool. Beitr., 44:19–31.

Calvert, W.H., L.E. Hedrick & L.P. Brower. 1979.
Mortality of the monarch butterfly, *Danaus plex-
ippus*: avian predation at five over-wintering sites
in Mexico. Science, 204:847–851.

Capocasale, R. & L. Bruno-Trezza. 1964. Biologia
de *Acanthopachylus aculeatus* (Kirby, 1819),
(Opiliones; Pachylinae). Rev. Soc. Uruguaya En-
tomol., 6:19–32.

Cockerill, J.J. 1988. Notes on aggregations of
Leiobunum (Opiliones) in the Southern U.S.A. J.
Arachnol., 16:123–126.

Coddington, J.A., M. Harner & E.A. Soderstrom.
1990. Mass aggregation in tropical harvestmen
(Opiliones, Gagrellidae: *Prionostemma* sp.). Rev.
Arachnol., 8:213–219.

Cokendolpher, J.C. 1987. Observations on the de-
fensive behaviors of a Neotropical Gonyleptidae
(Arachnida, Opiliones). Rev. Arachnol., 7:59–
63.

Duncan, P. & N. Vigne. 1979. The effect of group
size in horses on the rate of attacks by blood-
sucking flies. Anim. Behav., 27:623–625.

Foster, W.A. & J.E. Treherne. 1981. Evidence for
the dilution effect in the selfish herd from fish
predation on a marine insect. Nature, 295:466–
470.

Holmberg, R.G., N.P.D. Angerilli & J.L. Lacasse.
1984. Overwintering aggregation of *Leiobunum
paessleri* in caves and mines (Arachnida, Opili-
ones). J. Arachnol., 12:195–204.

Joly, A.B. 1970. Conheça a vegetação brasileira.
São Paulo: Editora da Universidade de São Paulo
- Ed. Polígono S.A. 250 pp.

Krebs, J.R. & N.B. Davies. 1993. An Introduction
to Behavioural Ecology. Blackwell, Oxford. 3rd
ed.

Pinto-da-Rocha, R. 1993. Invertebados caverníco-
las da porção meridional da província espeleo-
lógica do Vale do Ribeira, sul do Brasil. Rev.
Brasileira Zool., 10:229–255.

Roach, B., T. Eisner & J. Meinwald. 1980. Defen-
sive substances of opilionids. J. Chem. Ecol., 6:
511–516.

Glauco Machado: Museu de História Nat-
ural da Universidade Estadual de Campinas,
Instituto de Biologia, CEP 13081-970,
Caixa Postal 6190, Campinas, São Paulo,
Brazil

Carlos Henrique F. Vasconcelos: Univer-
sidade Federal de Minas Gerais, Instituto de
Ciências Biológicas, Departamento de
Zoologia, Belo Horizonte, Minas Gerais,
Brazil

RESEARCH NOTE

COOPERATIVE PREY CAPTURE IN THE COMMUNAL WEB SPIDER, *PHILOPONELLA RAFFRAYI* (ARANEAE, ULOBORIDAE)

Prey capture advantage has played an important role in the evolution of communal or social spiders (Shear 1970; Rypstra 1985, 1986; Buskirk 1981; Uetz 1986, 1989). Communal web organization may improve prey capture in two ways: 1) it may improve the ability of webs to intercept prey (the "ricochet effect") (Uetz 1989), and 2) it opens the possibility of communal prey immobilization that may allow spiders to capture larger and presumably more profitable prey. Communal capture of large insect prey has been observed in a number of social web-building spiders, such as *Agelena consociata* Denis 1965 (Krafft 1969), *Anelosimus eximius* (Keyserling 1884) (Vollrath & Rohde-Arndt 1983; Christenson 1984; Pasque & Krafft 1992), *Mallos gregalis* (Simon 1909) (see Jackson 1979), and it has been demonstrated that communal spiders capture larger prey than solitary spiders (Buskirk 1981; Nentwig 1985; Uetz 1986).

Members of the genus *Philoponella* Mello-Leitão are known to construct communal webs, but most have been reported to employ only non-cooperative prey capture (see Burgess 1978; Buskirk 1981; Smith 1982; Lubin 1986). However, cooperative prey capture has been reported in a few species of *Philoponella* (see Breitwisch 1989; Binford & Rypstra 1992). To understand the diversity of cooperative prey capture and social behavior in the genus *Philoponella,* the prey capture behavior of as many species as possible should be described.

This study describes the colony composition and prey capture handling behavior of the uloborid spider *Philoponella raffrayi* (Simon 1891) and determines if the efficiency with which they capture large insects is higher when spiders hunting cooperatively than when they hunt singly.

Philoponella raffrayi is a communal web-building spider that occupies the tropical rain forest undergrowth of peninsular Malaysia (Simon 1891; Masumoto 1992). I studied this species in the Pasoh Forest Reserve in Negri Sembilan state, Malaysia. A colony of *P. raffrayi* is composed of individual orb-webs connected to one another by non-adhesive silk. All uloborids lack poison glands and must rely on wrapping to subdue prey (Lubin 1986). The average body length of this species is 6.21 mm in females and 3.15 mm in males (Masumoto 1992). The volume of colonies is variable according to the number of individuals in the colony (Table 1). The age of adult females is easily determined by their body color. Adult females are orange for at least a week after the final molt, becoming black a few weeks later.

I conducted field observations in a 2 ha research area from February–April 1992 and also in March 1993. All colonies found within this area were included in the study. To locate these colonies, I searched within the study area for 3 days before the 25 February and the 17 March study periods. All observations were made between 0800–1800 h, which corresponded to the daylight periods in this area. I recorded the number, stage of maturation and behavior of spiders in colonies on 25 February and 17 March 1992. In March 1993, I also conducted a total of 17 hours of field observations on the only colony (4♂33♀) still present in the study area. For this colony, I recorded the stage of maturation, relative body length of interacting individuals and each insect that entered the colonial web. Individuals were not marked and the relative body length between the spider and the insect prey was estimated by eye. I collected females and their egg sacs from the No. 2 colony described below. I preserved them in 70% alcohol and counted the number of eggs per egg sac and,

Table 1.—The composition of *Philoponella raffrayi* in the research area of Pasoh Forest Reserve on 25 February and 17 March 1992. Between the two dates, colonies #7 and 8 disappeared, and the new colonies #9, 10, 11, 12 appeared in the study area. The asterisk (*) or double asterisks (**) indicates the number of *Argyrodes* spp. or *Portia* spp., respectively. The single dagger (†) indicates that of 24 females, 17 had produced eggsacs by 17 March.

Colony No.	25 February 1992					17 March 1992					
	No. of adult females (A)	No. of adult males (B)	No. of juveniles (C)	Other species	Colony size (cm) (length, width, height)	No. of adult females (D)	No. of adult males (E)	No. of juveniles (F)	Other species	Colony size (cm) (length, width, height)	Survivorship (D+E+F/ A+B+C)
1	0	0	28	0	30, 30, 60	20	1	0	0	40, 40, 60	75%
2	24	1	0	1*	60, 60, 60	24†	1	0	4*	70, 60, 70	100%
3	25	7	0	0	55, 55, 32	23	1	0	1*, 1**	60, 60, 35	75%
4	0	0	35	0	20, 15, 30	0	0	25	0	40, 40, 60	71%
5	44	2	0	0	70, 40, 70	44	0	0	0	200, 150, 150	96%
6	6	0	0	0	10, 15, 15	4	0	0	0	30, 20, 20	67%
7	15	0	0	0	40, 40, 40	—	—	—	—		—
8	15	5	0	0	30, 30, 30	—	—	—	—		—
9	—	—	—	—		28	2	0	1**	80, 80, 80	—
10	—	—	—	—		4	0	0	0	40, 40, 40	—
11	—	—	—	—		3	0	0	2*	20, 20, 20	—
12	—	—	—	—		14	1	0	0	40, 50, 40	—

Table 2.—The number of prey entering the colony, captured or not captured, in a colony of *Philoponella raffrayi*. Relative prey size is the ratio of prey body length to spider body length.

Relative prey size (prey/ spider)		Single	Cooper- ative
<0.1	Success	30	1
	Fail	1	0
	Efficiency (%)	97	100
0.1–0.5	Success	32	2
	Fail	4	0
	Efficiency (%)	89	100
0.5–1.0	Success	1	4
	Fail	11	0
	Efficiency (%)	8	100
1.0<	Success	0	0
	Fail	6	0
	Efficiency (%)	0	—

Figure 1.—The correlation between the cephalothorax width of females and the number of eggs deposited. Spearman's rank correlation: $Rs = 0.523$, $n = 15$. $P = 0.046$.

under a binocular microscope, measured to the nearest 0.1 mm the width of females' cephalothorax. Two of them were deposited as voucher specimens in the collection of the Department of Zoology, National Science Museum, Tokyo (NMST-Ar 3514, 3525). Capture efficiency is defined as the ratio of the number of insects captured compared to the number of insects entering the webs.

I observed eight colonies in February and ten colonies in March 1992 (Table 1). Each colony consisted of members of a similar developmental stage, apparently representing only variation in size of the same instar. Between 25 February–17 March (3 weeks), six of the eight colonies remained at the same web site, but two colonies disappeared from the study area and four colonies newly appeared. In March 1992, females of No. 2 colony produced twig-like egg sacs, hung them from the hub and began guarding the eggs. The mean number of eggs per egg sac was 118 ±9.96 ($\bar{x}$ ±SD, $n = 15$). This value was correlated with the cephalothorax width of its mother (Spearman's rank correlation; $Rs = 0.523$, $n = 15$, $P = 0.046$; Fig. 1). However, 8 of 13 females measured had a cephalothorax width of 1.5 mm but produced 101–132 eggs. Factors that may have contributed to the difference would be energy gain during the adult stage. Oviposition occurred between March–
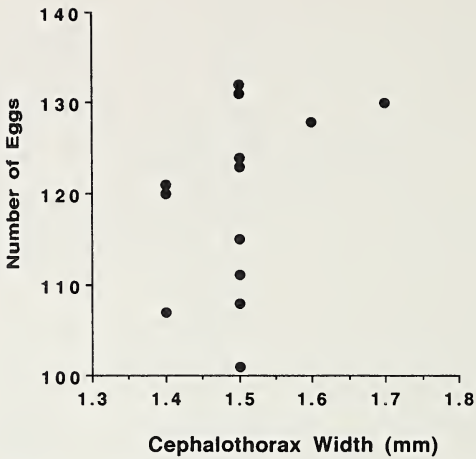
April in 1992, and he juveniles remained in the same colony where they had hatched. Developmental stages of females were synchronous within the same colony, but not synchronous among different colonies. Furthermore, the number of spiders in the same colony never increased, and no fusion of colonies was observed. During April, no colonies remained at the same web site and three colonies, each containing more than 100 juvenile *P. raffrayi*, appeared at different web sites. All adult females disappeared from the juvenile web colony, and I could detect no parent-offspring interaction except for egg sac guarding. Furthermore, *Argyrodes* and *Portia* were found in the colonies.

During the observation, I recorded 92 insects of four orders entering webs; Diptera (75), Hymenoptera (15), Coleoptera (1), Lepidoptera (1 larva). Of these insects, the spiders captured 66 Diptera, two Hymenoptera, one Coleoptera and one larva of Lepidoptera. Wrapping was dominantly conducted by individual females. However, when prey was trapped in the periphery of an individual orb web, 7 out of 70 prey items (10%) were wrapped by two cooperating females. They first subdued prey by throwing silk on it from a distance and began to more tightly wrap prey cooperatively as they rotated it. The prey capture efficiency of a single females was 89–97% when prey size was less than the half the

body length of the spider, but this decreased to only 8% when the relative prey size was between 0.5–1, and no prey was captured when the prey length was greater than spider body length. However, cooperative prey capture by two females resulted in 31% prey capture efficiency when the relative prey size was between 0.5–1 spider length, which was higher than that by a single female (Fisher's exact probability = 0.0027; Table 2). Even in cases where two females caught prey cooperatively, only one female fed on the prey item. In six out of seven cases, females that were larger by 10% of body length and more matured females fed alone on the captured prey. The effect of web ownership on the advantage in taking over a prey could not determined because I could not discriminate the owner from the intruder.

Communal uloborid spiders, such as *Philoponella oweni* Chamberlin 1924 were thought to lack any cooperative prey capture behavior (Buskirk 1981). However, cooperative prey capture has since been reported in a species of *Philoponella* in the Cameroon (Breitwisch 1989), and for *P. republicana* Simon 1891 (see Binford & Rypstra 1992). The prey capture by *P. raffrayi* is similar to that of *P. republicana,* except that no more than two individuals were observed to share in this behavior. These results indicate that there may several types of cooperative prey capture in the genus *Philoponella.*

LITERATURE CITED

Binford, G.J. & A.L. Rypstra. 1992. Foraging behavior of the communal spider, *Philoponella republicana* (Araneae: Uloboridae). J. Insect. Behav., 5:321–335.

Breitwisch, R. 1989. Prey capture by a West African social spider (Uloboridae: *Philoponella* sp.). Biotropica, 21:359–363.

Burgess, J.W. 1978. Social behavior in group-living spider species. Symp. Zool. Soc. London., 42:69–78.

Buskirk, R.E. 1981. Sociality in the Arachnida, Pp. 281–367. *In* Social Insects. Vol. II (H.R. Hermann, ed.). Academic Press, London, New York.

Christenson, T.E. 1984. Behavior of colonial and solitary spiders of the theridiid species *Anelosimus eximius.* Anim. Behav., 32:725–734.

Jackson, R.R. 1979. Predatory behavior of the social spider *Mallos gregalis*: Is it cooperative? Insectes Sociaux, 26:300- -312.

Krafft, B. 1969. Various aspects of the biology of *Agelena consociata* Denis when bred in the laboratory. American Zool., 9:201–210.

Lubin, Y.D. & R.H. Crozier. 1985. Electrophoretic evidence for population differentiation in a social spider *Achaearanea wau* (Theridiidae). Insectes Sociaux, 32:297–304.

Lubin, Y.D. 1986. Web building and prey capture in Uloboridae, Pp. 132–170. *In* Spiders: Webs, Behavior, and Evolution.(W.A. Shear, ed.). Stanford Univ. Press, California.

Masumoto, T. 1992. The composition of a colony of *Philoponella raffrayi* (Uloboridae) in Peninsular Malaysia. Acta Arachnol., 41:1–4.

Nentwig, W. 1985. Social spiders catch larger prey: a study of *Anelosimus eximius* (Araneae: Theridiidae). Behav. Ecol. Sociobiol., 17:79–85.

Pasquet, A. & B. Krafft. 1992. Cooperation and prey capture efficiency in a social spider *Anelosimus eximius* (Araneae, Theridiidae). Ethology, 90:121–133.

Roeloffs, R. & S.E. Riechert. 1988. Dispersal and population-genetic structure of the cooperative spider, *Agelena consociata,* in West African rainforest. Evolution., 42:173–183.

Rypstra, A.L. 1985. Aggregation of *Nephila clavipes* (L.) (Araneae: Araneidae) in relation to prey availability. J. Arachnol., 13:71–78.

Rypstra, A.L. 1986. High prey abundance and a reduction in cannibalism: the first step to sociality in spiders (Arachnida). J. Arachnol., 14: 193–200.

Shear, W.A. 1970. The evolution of social phenomena in spiders. Bull. British Arachnol. Soc., 1: 65–76.

Simon, E. 1891. Observations bilogiques sur les Arachnides. I. Araignees sociables, *In* Voyage de M.E. Simon au Venezuela (decembre 1881–avril 1888). 11e Memoire. Ann. Soc. Entomol. France, 60:5–14.

Smith, D.R. 1982. Reproductive success of solitary and communal *Philoponella oweni* (Araneae: Uloboridae). Behav. Ecol. Sociobiol., 11:149–154.

Uetz, G.W. 1986. Web-building and prey capture in communal orb weavers. Pp. 207–231. *In* Spi-

ders: Webs, Behavior, and Evolution.(W.A. Shear, ed.). Stanford Univ. Press, California.

Uetz, G.W. 1989. The "ricochet effect" and prey capture in colonial spiders. Oecologia, 81:154–159.

Vollrath, F. & Rohde-Arndt, D. 1983. Prey capture and feeding in the social spider *Anelosimus eximius*. Z. Tierpsychol., 61:334–340.

Toshiya Masumoto: Center for Ecological Research, Kyoto University; 4-1-23, Shimosakamoto, Otsu, Shiga, 520-01, Japan

RESEARCH NOTE

RAPD PROFILING OF SPIDER (ARANEAE) DNA

We present protocols and conditions for specimen storage, DNA extraction and storage, and the subsequent RAPD (Random Amplified Polymorphic DNA) profiling of spiders. Three common UK species, *Lepthyphantes tenuis* (Blackwall 1852), *Enoplognatha ovata* (Clerk 1757) and *Clubiona reclusa* (Cambridge 1863), members of the Linyphiidae, Theridiidae and Clubionidae respectively, were chosen to serve as examples with this highly adaptable technique.

Despite numerous reservations regarding the repeatability, homology, and statistical analysis of the data (see Grossberg et al. 1996 for a comprehensive review), RAPD profiling (Williams 1990) is still the method of choice for many researchers looking to address a wide range of ecological issues in an equally diverse array of organisms. RAPD data have enabled insights into population structure (e.g., Haymer & McInnis 1994; Kambhampati et al. 1992), geographical origins and invasion routes of colonizing species (e.g., Williams et al. 1994), the distinction of new genotypes of parasites (e.g., Majiwa et al. 1993) and conservation genetics (e.g., Rosetto et al. 1995). The RAPD technique can also be a useful initial step in detecting other classes of DNA marker such as microsatellites (Ender et al. 1996).

RAPD profiling is adopted despite the reservations because it possesses many advantages over other molecular marker systems, *viz.*, it is relatively fast and technically undemanding, screens the entire genome for polymorphisms, and can produce a potentially limitless number of markers (simply by screening with more primers). Moreover, due to the amplification process during the PCR thermal cycling, only minute quantities of DNA are required as template, making the analysis of invertebrates unproblematic, e.g., microhymenoptera (Landry et al. 1993).

Sample storage prior to DNA extraction was found to be the most crucial stage for this otherwise robust technique, which worked successfully with all the species tested (Fig. 1). Spiders were collected via a D-Vac suction sampler, or by hand, and returned to the lab alive. They were then either stored in ethylene glycol or 70% ethanol at room temperature, or frozen in liquid nitrogen and stored at −80 °C. DNA was extracted after three weeks and examined on a 1% agarose minigel. RAPD reactions were then carried out with DNA stored at 4 °C and −20 °C over a period of one month, to assess the optimal storage for extracted DNA.

Ethylene glycol and 70% ethanol were both found to be poor preservative media for the spider DNA, which had degraded substantially after three weeks storage at room temperature. Storage at −80 °C was found to be the most effective method tested for preserving specimens (at least for one year) prior to DNA extraction if extractions could not be made immediately (Fig. 2). However, it was necessary to identify the spiders prior to storage at −80 °C, as the delicate tissues of the epigyna and palps darkened following freezing, making identification more difficult. Saturated salt solutions have also been used by a number of authors as a means of preserving DNA during field collection of samples, e.g., (Seutin et al. 1991) but these were not investigated in this study.

Storage of extracted DNA at −20 °C is recommended if the sample is not to be used directly, as DNA held at 4 °C gave more variable results over time (results not shown). Fresh dilutions of DNA should be prepared from −20 °C stock prior to each RAPD reaction to ensure repeatability of profiles (Fig. 3).

The DNA extraction was carried out as follows. A 1.5 ml Eppendorf tube containing an adult spider was lowered into liquid nitrogen for 10 sec and the spider tipped out onto a Petri dish lid. The abdomen was removed with a sterile scalpel blade, preventing the possible
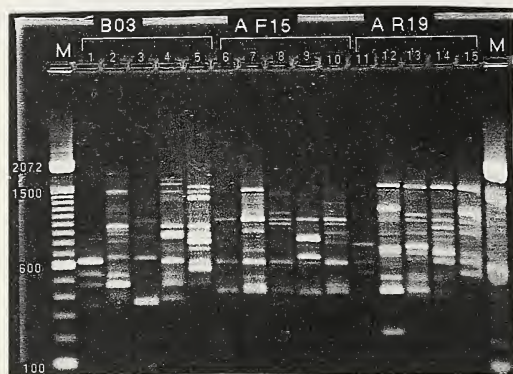
Lepthyphantes tenuis

Enoplognatha ovata

Clubiona reclusa

Figure 1.—RAPD profiles produced with three primers (chosen at random from those available in the laboratory) from five individuals from each species. Primer sequences are: OPB–O3 (5'–CATCCCCCAG–3'); OPAF–15 (5'–CACGAACCTC–3') and OPAR–19 (5'–CTGATCGCGG–3'). M = marker (size in base pairs).

amplification of DNA from prey ingested by the spider or of any parasitic burden. The carapace was then returned to the tube and refrozen. The carapace was homogenized with a sterile plastic Eppendorf pestle (a separate pestle was used for each sample to prevent cross contamination), 500μl chilled DNA extraction buffer (200mM Tris-HCl (pH 8.0), 70mM EDTA, 2M NaCl, 20mM sodium metabisulphite) and 90μl 5% sarcosyl solution added (Cheung et al. 1993), then additional grinding carried out to ensure complete destruction of tissue. The addition of Proteinase K and RNAse was not found necessary to extract DNA which amplified to produce clear repeatable profiles. The tubes were then incubated at 65 °C for 1 h with occasional mixing by inversion. Following incubation, the homogenized tissue was spun in a microfuge at 16,000 × g for 3 min to pellet gross debris, and the supernatant, containing the DNA, was transferred to a fresh tube. To precipitate the DNA, 90μl of 10M ammonium acetate and 500μl of chilled isopropanol were added to the supernatant, the tube slowly inverted 50 times to mix, and the sample placed at −20 °C for 2 h.

Total precipitated DNA was pelleted at 16,000 × g for 10 min, after which the supernatant was poured off and 400μl 70% ethanol added to wash the pellet. Following a further 4 min spin the 70% ethanol was decanted. Finally, the pellet was air dried for 30–45 min then resuspended in 50μl sterile water (Sigma, UK). Resuspension was aided by heating to 60 °C for 1 h. The quantity of the DNA recovered, as observed on a 1% agarose minigel, was comparable with DNA extracted using the more traditional, solvent extraction method, whilst avoiding the unpleasantness of handling phenol and chloroform.

DNA amplification was carried out on a Perkin Elmer TC-1 thermal cycler, using a step cycle, programmed for 35 cycles of 1 min at 95 °C for DNA denaturation, 1 min at 36 °C for primer annealing, and 2 min at 72 °C for primer extension. This was preceded by an initial denaturation step of 2 min at 95 °C. The cycling was followed by a final primer extension step at 72 °C for 8 min. Following optimization of DNA and magnesium concentrations, in a 50μl reaction volume the following components were employed: 1X Perkin Elmer

(a)   (b)
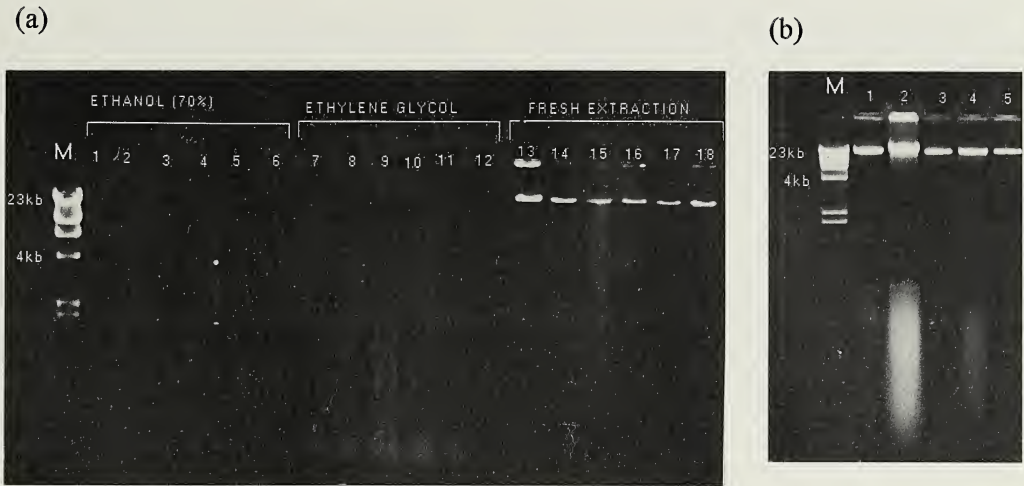

Figure 2.—Effect of specimen preservation on DNA. (a) DNA extractions from 18 *Lepthyphantes tenuis* stored for three weeks at room temperature in 70% ethanol (lanes 1–6), ethylene glycol (lanes 7–12, or recovered from fresh specimens (lanes 13–18). (b) Extraction from 5 *L.tenuis* stored at −80 °C for 12 months. M = marker (size in base pairs).

buffer, 3mM $MgCl_2$, 200μM each of dATP, dTTP, dCTP and dGTP, 0.5 units of Stoffel *Taq* and 0.2μM primer (10-base primers, Operon Technologies Inc., Alameda, California, USA). DNA template was present at a concentration of approximately 40ng per reaction, calculated by comparing by eye the intensity of ethidium bromide stained genomic extracts with dilutions of a DNA marker (λ/HindIII digest) whilst under UV illumination (Sambrook et al. 1989). This allowed dilutions of DNA to be made which were in a good approximation to each other. Finally, prior to PCR, the reaction mix was overlaid with approximately 25μl of mineral oil to prevent evaporation of the sample during cycling.

Amplified RAPD products were visualized on a 1.5% TAE agarose gel following electrophoresis at 80 volts for 2 h. The gel was stained with ethidium bromide (0.5μg/ml) for 20–30 min, rinsed briefly, then examined on a UV illuminator. The results were captured using the IS500 digital image analysis system (Flowgen, UK).

Sample storage in ethanol for future DNA extraction is something of a contentious issue, with reports ranging from vertebrate tissues stored for six years producing good yields of high molecular weight DNA (Smith et al. 1987), to Coleopteran DNA which maintained its integrity for only six weeks in 95% ethanol (Reiss et al. 1995). Laulier et al. (1995) state
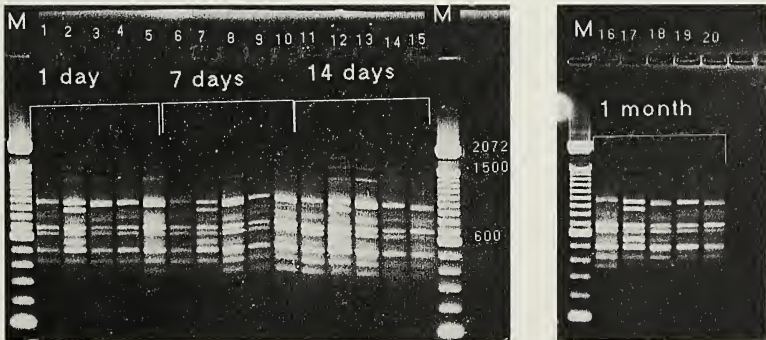

Figure 3.—Reproducibility of RAPD markers over time. Profiles from stock DNA extractions stored at −20 °C with primer, OPAR–19. Five *Enoplognatha ovata* after 1 day (lanes 1–5), 7 days (lanes 5–10), 14 days (lanes 11–15) and one month (lanes 16–20). M = marker (size in base pairs).

that DNA can be recovered from ethanol and methanol preserved samples, but the degree of degradation appears to be species specific, and the yield is generally poor. It can be speculated that any species specificity of degradation may be due to the physical properties of the cuticle of the organism. Ito (1992) reported that unknown contaminants in 100% ethanol can cause degradation of DNA, leading to the simple classification of ethanols as "good" and "bad". Our findings support the difficulty of finding a "good" ethanol and it may be prudent not to take the risk if possible.

In summary, this preliminary study has shown that following optimization, the RAPD technique produces clear and repeatable results and is readily applicable to arachnological studies. Molecular data from such studies should allow new insights into a number of ecological issues if applied appropriately.

LITERATURE CITED

Cheung, W.Y., N. Hubert & B.S. Landry. 1993. A simple and rapid DNA extraction method for plant, animal, and insects suitable for RAPD and other PCR analysis. PCR Methods and Applications, 3:69–70.

Ender, A., K. Schwenk, T. Stadler, B. Streit & B. Schierwater. 1996. RAPD identification of microsatellites in *Daphnia*. Mol. Ecol., 5:437–441.

Grossberg, R.K., D.R. Levitan & B.B. Cameron. 1996. Characterization of genetic structure and geneologies using RAPD-PCR markers: A random primer for the novice or nervous. Pp.67–100, *In* Molecular Zoology: Advances, Strategies, and Protocols. (Joan D.& S.R. Palumbi, eds.). Wiley-Liss, Inc.

Haymer, D.S. & D.O. McInnis. 1994. Resolution of populations of the Mediterranean fruit fly at the DNA level using random primers for the polymerase chain reaction. Genome, 37:244–248.

Ito, K. 1992. Nearly complete loss of nucleic acids by commercially available highly purified ethanol. Biotechniques, 12 (1):69–70.

Kambhampati, S., W.C. Black & K.S. Rai. 1992. Random amplified DNA of mosquito species and populations (Diptera: Calicidae): Techniques, statistical analysis and applications. J. Med. Entomol., 29:939–945.

Landry, B.S., L. Dextraze & G. Boivin. 1993. Random amplified polymorphic DNA markers for DNA fingerprinting and genetic variability assessment of minute parasitic wasp species (Hymenoptera: Mymaridae and Trichogrammatidae)

used in biological control programs of phytophagous insects. Genome, 36:580–587.

Laulier, M., E. Pradier, Y. Bigot & G. Periquet. 1995. An easy method for preserving nucleic acids in field samples for later molecular and genetic studies without refrigerating. J. Evol. Biol., 8:657–663.

Majiwa, A.O., M. Maina, J.N. Waitumbi, S. Mihok & E. Zweygarth. 1993. *Trypanosoma (Nannomonas) congoloense*: Molecular characterization of a new genotype from Tsavo, Kenya. Parasitology, 106:151–162.

Reiss, R.A., D.P. Schwert & A.C. Ashworth. 1995. Field preservation of Coleoptera for molecular genetic analysis. Env. Entomol., 24:716–719.

Rossetto, M., P.K. Weaver & K.W. Dixon. 1995. Use of RAPD analysis in devising conservation strategies for the rare and endangered *Grevillea scapigera* (Proteaceae). Mol. Ecol., 4:321–329.

Sambrook, J., E.F. Fritsch & T. Maniatis. 1989. Molecular Cloning: A Laboratory Manual, 2nd ed., section E5. Cold Spring Harbor Laboratory, Cold Spring Harbor, New York.

Seutin, G., B.N. White & P.T. Boag. 1991. Preservation of avian blood and tissue samples for DNA analysis. Canadian J. Zool., 69:82–90.

Smith, L.J., R.C. Braylan, J.E. Nutkis, K.B. Edmundsen, J.R. Downing & E.K. Wakeland. 1987. Extraction of cellular DNA from human cells and tissues fixed in ethanol. Analy. Biochem., 169:135–138.

Stiller, J.W. & A.L. Denton. 1995. One hundred years of *Spartina alterniflora* (Poaceae) in Willapa Bay, Washington: Random amplified polymorphic DNA analysis of an invasive population. Mol. Ecol., 4:355–363.

Williams, J.G.K., A.R. Kubelick, J. Livak, J.A. Rafalski & S.V. Tingey. 1990. DNA polymorphisms amplified by arbitrary primers are useful as genetic markers. Nuc. Acid Res., 18:6531–6535.

Williams, C.L., S.L. Goldson, D.B. Baird & D.W. Bullock. 1994. Geographical origin of an introduced insect pest, *Listronotis bonariensis* (Kuschel), determined by RAPD analysis. Heredity, 72:412–419.

Stuart A'Hara[1], Rob Harling, Rod McKinlay and **Chris Topping[2]:** Crop Science and Technology Dept., Scottish Agricultural College, West Mains Road, Edinburgh, EH9 3JG UK.

[1] To whom correspondence should be addressed.
[2] NERI, Landscape Ecology Dept, Kalo, Grenavej 14, Rondo, Denmark.

RESEARCH NOTE

SEXUAL DIFFERENCES IN METABOLIC RATES OF SPIDERS

In general, spiders are considered to exhibit resting metabolic rates about half of those measured for other poikilothermic animals of equal mass (e.g., Anderson 1970; Greenstone & Bennett 1980; Anderson & Prestwich 1982; Anderson 1987; Paul et al. 1989; Anderson 1996). However, these metabolic rates were all compared to Hemmingsen's poikilotherm mass-scaling equation (1960), which has recently been shown to systematically overestimate metabolism in small animals (Lighton & Fielden 1995). Thus, almost any data on standard metabolic rates result in low values of metabolic rate compared to this equation. More directly, Lighton & Fielden (1995) further showed that metabolic rates for spiders (22 genera) do not differ from those of ants [Formicidae (10 genera)] and beetles [Tenebrionidae (8 genera)] of comparable size. However, under prolonged starvation spider metabolic rates may be below the standard metabolic rate (Itô 1964; Nakamura 1972; Anderson 1974), thus making them well adapted to environments with unpredictable food availability.

Almost all studies on spider metabolic rates have used only adult females (Table 1). This may be due mainly to the very influential paper on the field by Anderson (1970). He reasoned that using juveniles or males may complicate the data because the growth of the juveniles or the relatively high activity patterns of males may affect oxygen consumption. However, given the many differences in life-history characteristics between female and male spiders in general (e.g., size, longevity, reproductive efforts), it might be possible that there are also ecologically significant differences in energy consumption between females and males. Indeed, Edgar (1971) reported differences in female and male growth efficiency (ratio food consumed/weight increase) in *Pardosa lugubris* (Walkenaer); and Bromhall (1987), having found a significant difference in heart-rates between males and females of

Argyroneta aquatica (Clerck), suggested that the sexes may have different energetic capacities. Furthermore, if females are in the reproductive state and producing eggs, it may well be that the data collected from them is not less complicated than data from juveniles or males.

In this study my aim was to compare the available data on spider metabolism from literature and present data comparing the resting CO_2 production rate of females and males in the wolf spider *Hygrolycosa rubrofasciata* (Ohlert 1865) (Lycosidae).

Hygrolycosa rubrofasciata were collected from a bog at Sattanen, northern Finland, immediately after snow melt but before the mating activities began in late May 1996. Throughout the study spiders were housed in individual plastic jars in which food and water were available continuously. Because spiders were not fasting the levels of resting CO_2 production may be overestimates, but this may not affect the comparison between males and females.

CO_2 production rates were measured with a flow-through respirometry utilizing CO_2 analyzer model LI-6251 connected to Sable Systems data acquisition and analysis software Datacan V (Sable Systems, Salt Lake City, Utah). Spiders were inserted into a cylinder-shaped test chamber (length 50 mm, diameter 13 mm) plugged at both ends with a rubber plug. From the incoming air CO_2 and moisture were removed by filtering the air through soda lime and silica gel before it went into the test chamber. From the test chamber the air with CO_2 produced by the spider flowed through another moisture absorbing silica gel filter to the CO_2 analyzer. The air flow was 150 ml per minute and it did not seem to disturb spiders. All the measurements were made at the temperature of 25 °C.

The CO_2 production of resting spiders was measured several times during different days. I analyzed only those measurements that were

Table 1.—Number of spider species studied. Only studies measuring directly the CO_2 production or O_2 consumption were included; studies on heart-rates were excluded sine there is no clear-cut relationship between heart-rate and metabolic rate in spiders (see e.g., Carrel & Heathcote 1976; Greenstone & Bennett 1980; Anderson & Prestwich 1982; Carrel 1987). Altogether I could find 31 studies examining 83 species belonging to 57 genera and to 19 families.

	Number of species
Female only	69
Male only	0
Both sexes	8
Sex not reported	6
Total	83

taken after the spider had been motionless for at least 5 min. Each valid measure was a mean CO_2 production over a period of 2–5 min. The number of measurements per spider ranged from 1 to 9 and the total time measurements lasted ranged from 2–44 min. In the analysis I used a mean value from all of the valid measurements. Between the measurements the test chamber was washed with water and dried with soft cellulose paper.

In addition to CO_2 production I measured the wet mass of the individuals. After finishing the metabolic rate measurements also dry mass was measured separately for the prosoma and opisthosoma.

I found a significant difference in female and male resting CO_2 production rates: females had 47% higher resting CO_2 production rate per mass unit than males (Table 2). However, the regression slopes of CO_2 production per mass unit and body mass did not differ between females and males ($t = 0.01$, $df = 33$, $P = 0.9$). Similarly, neither of the slopes was significantly different from zero-slope

(females: $t = 0.28$, $df = 5$, $P > 0.7$; males: $t = 1.73$, $df = 28$, $P = 0.095$).

In this data set female and male wet body mass did not differ (Table 2). However, even though there was a strong and significant correlation between the wet and dry body mass in both sexes (female: Pearson's $r = 0.87$, $n = 7$, $P = 0.011$; male: Pearson's $r = 0.91$, $n = 28$, $P << 0.001$), females had a significantly higher dry body mass than males (Table 2). The difference between the sexes was even more pronounced when calculated for the ratio dry mass/wet mass (two sample t-test: $t = 11.05$, $df = 33$, $P << 0.001$). Females had also higher opisthosoma/prosoma dry mass ratio than males (two sample t- test: $t = 4.73$, $df = 6.9$, $P = 0.002$).

My results demonstrate that there are differences in resting CO_2 production rates between the sexes in the wolf spider *H. rubrofasciata*. The difference between sexes in resting metabolic rates is also supported by the only study so far measuring adult male spiders in any extent (Watson & Lighton 1994). They found that in *Linyphia litigiosa* (Keyserling) (Linyphiidae) male resting metabolic rate is 161% of female resting metabolic rate. Also, in *Pardosa astrigera* (L. Koch) (Lycosidae) males seemed to have higher metabolic rates than females, but no statistical analysis were presented (Tanaka & Itô 1982). In my study male resting CO_2 production rate was only 63% of female resting CO_2 production rate. One possible explanation is that females may have been in a different reproductive state: there is likely to be a significant difference in female metabolic rate during reproductive season and between reproductive seasons. One other explanation for the difference may be that in Watson & Lighton's (1994) study the male resting metabolic rate was measured within few days after copulation (i.e., after males were involved in sex-

Table 2.—Means and standard errors for CO_2 production (ml g^{-1} h^{-1}), wet body mass (mg) and dry body mass (mg) separately for males and females. Test statistics come from two-sample t-tests between males and females.

	Males	Females	t	df	P
Sample size	30	7			
CO_2 production $\pm$ SE	0.221 ± 0.007	0.325 ± 0.016	6.33	35	$<<0.001$
Body mass wet $\pm$ SE	21.15 ± 0.70	19.86 ± 0.67	1.05	19.6	>0.3
Body mass dry $\pm$ SE	3.80 ± 0.15	5.07 ± 0.26	3.97	33	<0.001

ual activities), while in my study males were not allowed to copulate prior to measurements. Copulation might affect male activity levels. In any case differences between sexes in metabolic rates of spiders can not be generalized with the results from the very few studies available.

Female *H. rubrofasciata* had higher dry mass/wet mass ratio, and higher dry opisthosoma mass/dry prosoma mass ratio than males. The latter ratio is easily explained by the morphological difference between female and male abdomens: females have larger abdomens than males. The former ratio, however, is more complicated. It suggests that females have higher dry matter content per wet mass unit than males.

Organisms are mostly composed of lipids and proteins. Lipids generally contain approximately 20% water while proteins contain approximately 80% water. Thus, the difference in the dry mass/wet mass ratio indicates that females and males contain different ratios of these materials. Since females use lipids in egg production, it is not surprising to find such a difference in dry mass/wet mass ratios between sexes. These results are consistent with the study by Carrel (1990) examining the water content in the wolf spider *Lycosa ceratiola* Gertsch & Wallace. He reported a similar difference in dry mass between the sexes and came to the same conclusion that—because of the egg production—females may contain more lipids and thus less water than males.

In spiders there seem to be differences between sexes in heart-rate (Bromhall 1987), growth efficiency (Edgar 1971) and metabolic rate (Tanaka & Itô 1982; Watson & Lighton 1994; this study; but see Humphreys 1977 for no difference). In fact, most metabolic rate studies where both female and male spiders were studied, have found differences between the sexes. However, available literature has concentrated solely on female spiders (Table 1). Therefore, before extrapolating from the results of metabolic rates of one sex to comprehend the whole species or larger taxonomic groups, one should carefully consider the possible differences between sexes. Studying more closely these differences between sexes could give us some insight to the often so different life history strategies of female and male spiders.

LITERATURE CITED

Anderson, J.F. 1970. Metabolic rates of spiders. Comp. Biochem. Physiol., 33:51–72.

Anderson, J.F. 1974. Responses to starvation in the spiders *Lycosa lenta* Hentz and *Filistata hibernalis* (Hentz). Ecology, 55:576–585.

Anderson, J.F. 1987. Morphology and allometry of the purse-web of *Sphodros abboti* (Araneae, Atypidae): Respiratory and energetic considerations. J. Arachnol., 15:141–150.

Anderson, J.F. 1994. Comparative energetics of comb-footed spiders (Araneae: Theridiidae). Comp. Biochem. Physiol., 109A:181–189.

Anderson, J.F. 1996. Metabolic rates of resting salticid and thomisid spiders. J. Arachnol., 24:129–134.

Anderson, J.F. & K.N. Prestwich. 1982. Respiratory gas exchange in spiders. Physiol. Zool., 55:72–90.

Anderson, J.F. & K.N. Prestwich. 1985. The physiology of exercise at and above maximal aerobic capacity in a theraphosid (tarantula) spider, *Brachypelma smithi* (F.O. Pickard-Cambridge). J. Comp. Physiol. B, 155:529–539.

Bromhall, C. 1987. Spider heart-rates and locomotion. J. Comp. Physiol. B, 157:451–460.

Carrel, J.E. 1987. Heart rate and physiological ecology. Pp. 95–110. *In* Ecophysiology of spiders. (W. Nentwig, ed.). Springer-Verlag. New York.

Carrel, J.E. 1990. Water and hemolymph content in the wolf spider *Lycosa ceratiola* (Araneae, Lycosidae). J. Arachnol., 18:35–40.

Carrel, J.E. & R.D. Heathcote. 1976. Heart rate in spiders: Influence of body size and foraging energetics. Science, 193:148–150.

Edgar, W.D. 1971. Aspects of the ecological energetics of the wolf spider *Pardosa* (*Lycosa*) *lugubris* (Walkenaer). Oecologia, 7:136–154.

Ford, M.J. 1977a. Energy costs of the predation strategy of the web-spinning spider *Lepthyphantes zimmermanni* Bertkau (Linyphiidae). Oecologia, 28:341–349.

Ford, M.J. 1977b. Metabolic costs of the predation strategy of the spider *Pardosa amentata* (Clerk) (Lycosidae). Oecologia, 28:333–340.

Greenstone, M.H. & A.F. Bennett. 1980. Foraging strategy and metabolic rate in spiders. Ecology, 61:1255–1259.

Hadley, N.F., G.A. Ahearn & F.G. Howarth. 1981. Water and metabolic relations of cave-adapted and epigean lycosid spiders in Hawaii. J. Arachnol., 9:215–222.

Hemmingsen, A.M. 1960. Energy metabolism as related to body size and respiratory surfaces, and its evolution. Rep. Steno Mem. Hosp. (Copenhagen), 9:1–110.

Humphreys, W.F. 1975. The respiration of *Geolycosa godeffroyi* (Araneae: Lycosidae) under conditions of constant and cyclic temperature. Physiol. Zool., 48:269–281.

Humphreys, W.F. 1977. Respiration studies on *Geolycosa godeffroyi* (Araneae: Lycosidae) and their relationship to field estimates of metabolic heat loss. Comp. Biochem. Physiol., 57A:255–263.

Itô, Y. 1964. Preliminary studies on the respiratory energy loss of a spider, *Lycosa pseudoannulata.* Res. Pop. Ecol., 6:13–21.

Lighton, J.R.B. & L.J. Fielden. 1995. Mass scaling of standard metabolism in ticks: a valid case of low metabolic rates in sit-and-wait strategists. Physiol. Zool., 68:43–62.

Lighton, J.R.B. & R.G. Gillespie. 1989. The energetics of mimicry: the cost of pedestrian transport in a formicinae ant and its mimic, a clubionid spider. Physiol. Entomol., 14:173–177.

Maya, M., S. Jaganathan & S.A. Karuppaswamy. 1981. Respiratory mechanism of the spider, *Hippasa pantherina* (Family: Lycosidae). Proc. Indian Acad. Sci. (Anim. Sci.), 90:539–543.

McQueen, D.J. 1980. Active respiration rates for the burrowing wolf spider *Geolycosa domifex* (Hancock). Canadian J. Zool., 58:1066–1074.

McQueen, D.J., L.K. Pannell & C.L. McLay. 1983. Respiration rates for the intertidal spider *Desis marina* (Hector). New Zealand J. Zool., 10:383–400.

Miyashita, K. 1969. Effects of locomotory activity, temperature and hunger on the respiratory rate of *Lycosa T- insignita* Boes. et Str. (Araneae: Lycosidae). Appl. Entomol. Zool., 4:105–113.

Myrcha, A. & B. Stejgwillo-Laudanska. 1970. Resting metabolism of *Araneus quadratus* (Clerc) females. Bull. L'Acad. Polonaise des Sci., Sér Sci. Biol., C1. II, 18:257–259.

Myrcha, A. & B. Stejgwillo-Laudanska. 1973. Changes in the metabolic rate of starved Lycosidae spiders. Bull. L'Acad. Polonaise des Sci., Sér. Sci. Biol. C1. II, 21:209–213.

Nakamura, K. 1972. The ingestion in wolf spiders. II. The expression of hunger and amount of ingestion in relation to spider's hunger. Res. Pop. Ecol., 14:82–96.

Paul, R., T. Fincke & B. Linzen. 1987. Respiration in the tarantula *Eurypelma californicum*: evidence for diffusion lungs. J. Comp. Physiol. B, 157:209–217.

Paul, R., T. Fincke & B. Linzen. 1989. Book lung function in arachnids. J. Comp. Physiol. B, 159:409–418.

Peakall, D.B. & P.N. Witt. 1976. The energy budget of an orb-web building spider. Comp. Biochem. Physiol., 54A:187–190.

Prestwich, K.N. 1983. The roles of aerobic and anaerobic metabolism in active spiders. Physiol. Zool., 56:122–132.

Tanaka, K. & Y. Itô. 1982. Decrease in respiratory rate in a wolf spider, *Pardosa astrigera* (L. Koch), under starvation. Res. Pop. Ecol., 24:360–374.

Watson, P.J. & J.R.B. Lighton. 1994. Sexual selection and the energetics of copulatory courtship in the Sierra dome spider, *Linyphia litigiosa.* Anim. Behav., 48:615–626.

Janne S. Kotiaho[1]: Department of Biological and Environmental Science, University of Jyväskylä, P.O. Box 35, FIN-40351 Jyväskylä, Finland.

[1]*Current address:* Department of Zoology, University of Western Australia, Nedlands, Western Australia 6009, Australia.

RESEARCH NOTE

INGESTED BIOMASS OF PREY AS A MORE ACCURATE ESTIMATOR OF FORAGING INTAKE BY SPIDER PREDATORS

Spiders have became more and more important as model organisms of foraging ecology (Uetz 1992; Wise 1993). Their foraging intake, especially that of orb-weaving spiders, can be easily estimated. These are sit-and-wait predators whose prey intake can be measured by examining insects trapped on webs. Furthermore, all spiders exhibit external digestion by injecting into the prey digestive juices which liquefy the inner soft parts. The spider retrieves the liquefied material by its sucking stomach, then discards the indigestible exoskeleton (Foelix 1982). Therefore, the spider's foraging intake can be accurately investigated by comparing biomass of prey before and after consumption.

This advantage has not been fully exploited in most spider foraging studies. Instead, dry weight of trapped prey calculated from length-weight equations given by Schoener (1980) is frequently used to estimate the spider's foraging intake. For example, Craig (1989) estimated the foraging intake between sympatric orb-weavers of different size; Cangialosi (1990) accessed the relative foraging intake of social spider hosts and kleptoparasites, and Higgins & Buskirk (1992) examined how prey intake affects foraging strategies of *Nephila clavata* L. Koch 1878. However, the biomass calculated from equations of Schoener (1980) includes both digestible soft parts and the indigestible exoskeleton, which does not seem to be appropriate considering how most spiders ingest food. Therefore, I estimated the biomass of temperate zone insects available for spider ingestion by comparing the weight of prey before and after spider consumption to provide a length-ingested biomass equation for future foraging studies. Moreover, I also evaluated total dry weight as an estimator of ingestible biomass by examining if those two variables associated with prey correlate well with each other.

This study was conducted in Matthaei Botanical Gardens of the University of Michigan in Ann Arbor, Michigan, USA in August 1995. Twenty cages (40 × 40 × 20 cm) were built from foam board and nylon screen, and each cage housed one female banded garden spider (*Argiope trifasciata* (Forskål 1775)) collected from the Gardens. During the study, insects were collected daily from the prairie at the Gardens by sweep netting. Before being given to spiders, insects were kept in vials then placed in a freezer for 5 minutes. After being removed from the vial and wiped dry with tissue paper, the insect body length was measured to the nearest 0.1 mm and weighed to the nearest 0.1 mg. Insects were placed on the webs of caged *A. trifasciata* before recovering from cooling. Each spider was given one insect each day, and size and taxa of prey each spider consumed were documented to ensure that all spiders received a similar array of prey, both in type and size. After 24 hours I collected the discarded exoskeletons from the cage bottoms then weighed the remains. I gave spiders new prey only after they dropped the consumed insect from their webs. The insect's weight after being consumed was subtracted from its original weight to give the ingested biomass.

I estimated body length–ingested biomass relationship by the following equation used by Schoener (1980):

(a) $$W = aL^b$$

In equation (a), W stands for ingested biomass, L for body length of prey, and a and b are parameters to be estimated. To estimate parameters a and b, (a) was log-transformed into:

(b) $$\log W = \log a + b \log L$$

A linear regression was calculated between log W and log L to generate statistics of parameters a and b (Schoener 1980). To examine the relationship between dry weight and in-

gested biomass of various insect taxa and size, body length data were transformed into dry weight using equations given by Schoener (1980). Schoener (1980) did not provide a temperate zone orthopteran dry weight equation, so I used the equation generated from orthopterans of Canas, Costa Rica (dry forest). I then plotted ingested biomass and dry weight values generated from body length of collected insects to examine the relationship between those two variables (Fig. 1).

Ingested biomass data were collected from 25 hymenopterans (ranging from 5–24 mm), 46 orthopterans (ranging from 6–28 mm), 13 dipterans (ranging from 5–10 mm), and 19 homopterans (ranging from 4–9 mm). Coleopterans were not included in the analysis because I could not collect sufficient insects. The ingested biomass - body length relationship of temperate zone prairie insects can be expressed as Hymenoptera: $W = 0.120L^{2.226}$, Orthoptera: $W = 0.382L^{1.972}$, Diptera: $W = 0.008L^{3.678}$ and Homoptera: $W = 0.014L^{3.233}$ (Table 1). Insect dry weight and ingested biomass did not correlate well with each other (Fig. 1). The deviation between estimated ingested biomass and dry weight widened as insect body length increased.

The increase in discrepancy between dry weight and digestible biomass as insect size increases can be explained by the following. Suppose the weights of three major components of an insect—water, digestible macromolecules and indigestible exoskeleton—can be described as functions of the insect size (S). Assume that a given type of insect is composed of 70% water, 20% exoskeleton and 10% macromolecules, and assume that this ratio is more or less constant for all size classes, then the total biomass of an insect of the size S can be described as:

$$\text{Total biomass} = f(S) = 0.7\ f(S) + 0.2\ f(S) + 0.1\ f(S).$$

The dry weight estimated from Schoener (1980) is composed mainly of exoskeleton and digestible macromolecules, and therefore can be described as $0.1\ f(S) + 0.2\ f(S) = 0.3\ f(S)$. However, the ingestible biomass of an insect is composed of both water and digestible macromolecules, therefore can be described as: $0.7\ f(S) + 0.1\ f(S) = 0.8\ f(S)$. The discrepancy between the dry weight and ingestible biomass of a given insect then is: 0.8
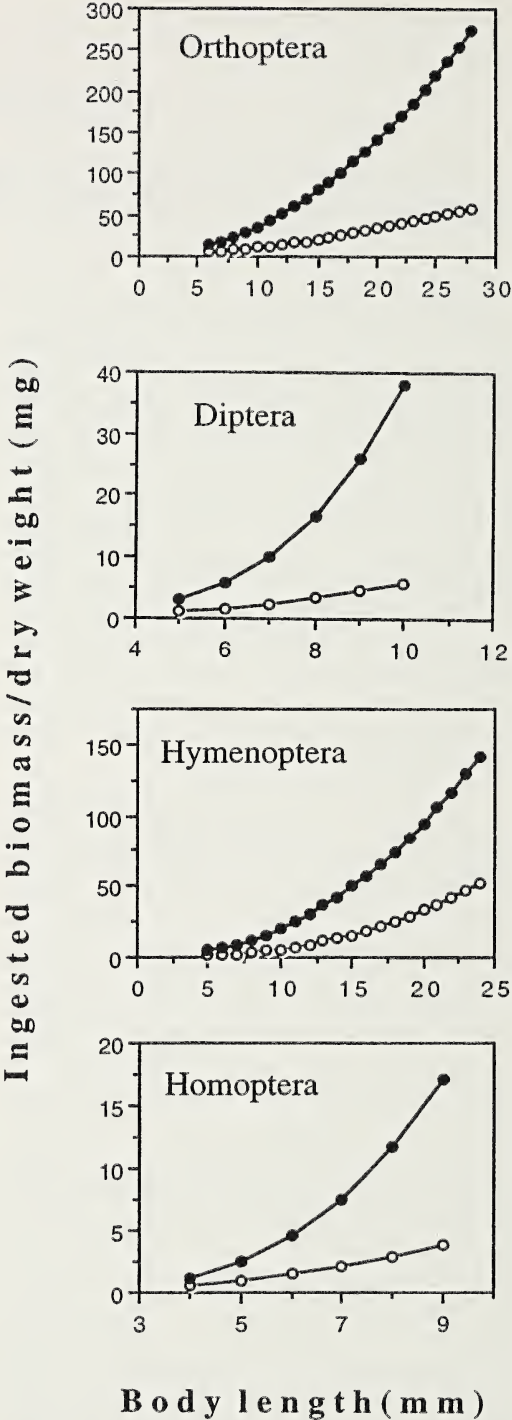

Figure 1.—Estimated ingested biomass (●) and dry weight (○) of temperate zone prairie insects. Length-weight equations used for dry weight estimation were Hymenoptera: $W = 0.016L^{2.55}$, Orthoptera: $W = 0.240L^{1.65}$, Diptera: $W = 0.022L^{2.42}$ and Homoptera: $W = 0.024L^{2.31}$, where W is the dry weight (mg) and L the body length (mm) of the insects.

Table 1.—Regression statistics for ingested biomass (mg) on body length (mm) of temperate prairie insects. Equation is logW = log a + blog L, r is the regression coefficient.

	n	r	P	log a ± SE	b ± SE
Hymenoptera	25	0.796	<0.001	−0.921 ± 0.400	2.226 ± 0.353
Orthoptera	46	0.883	<0.001	−0.417 ± 0.178	1.972 ± 0.158
Diptera	13	0.841	<0.001	−2.094 ± 0.617	3.678 ± 0.713
Homoptera	19	0.894	<0.001	−1.868 ± 0.316	3.233 ± 0.394

f(S) − 0.3 f(S) = 0.5 f(S). Therefore, the larger the size of an insect, the larger the value of f(S), and consequently generates a larger discrepancy between that insect's dry weight and digestible biomass.

The results of this study suggest that the length-weight equation provided by Schoener (1980), although traditionally used as a standard way of generating foraging intake of spiders, is not an accurate estimator. This is true especially since many spiders, such as *Nephila* (see Nentwig 1985) and *Argiope* (Murakami 1983), have a great range in prey size, thus the relative energy content of large prey would be greatly underestimated if determined by dry weight alone. The equations given by Schoener (1980) may be a good estimator of foraging intake if predators ingest whole prey. However, the unique food ingestion mode exhibited by spiders makes the length-weight equations provided by Schoener (1980) not entirely suitable for estimating their foraging intake. Future studies should consider using ingestible biomass of prey in estimating the foraging intake of spiders. To allow better and more accurate estimation of spider foraging gain in future studies, similar data for temperate zone coleopterans and various taxa of tropical insects are needed.

We greatly thank Mike Holmer and Jim Dickinson of the University of Michigan Matthaei Botanical Gardens for their kind support. Rachel Simpson of Department of Biology, University of Michigan kindly allowed the use of equipment in the Ecology Laboratory of the Gardens. Special thanks are given to Jim I. Liu for his dedicated assistance in the field and laboratory.

LITERATURE CITED

Cangialosi, K.R. 1990. The Behavioral and Ecological Interactions of the Kleptoparasitic Spider, *Argyrodes ululans,* and Its Social Spider host, *Anelosimus eximius.* Ph.D. dissertation, Miami University.

Craig, C.L. 1989. Alternative foraging modes of orb web weaving spiders. Biotropica, 21:257–264.

Foelix, R.F. 1982. Biology of Spiders. Harvard Univ. Press. Cambridge, Massachusetts.

Higgins L.E. & R.E. Buskirk. 1992. A trap-building predator exhibits different tactics for different aspects of foraging behavior. Anim. Behav., 44:485–499.

Murakami, Y. 1983. Factors determining the prey size of the orb-web spider, *Argiope amoena* (L. Koch) (Argiopidae). Oecologia, 57:72–77.

Nentwig, W. 1985. Prey analysis of four species of tropical orb-weaving spiders (Araneae: Araneidae) and a comparison with araneids of the temperate zone. Oecologia, 66:580–594.

Schoener, T.W. 1980. Length-weight regression in tropical and temperate forest-understory insects. Ann. Entomol. Soc. America, 73:106–109.

Uetz, G.W. 1992. Foraging strategies of spiders. TREE, 7:155–159.

Wise, D.H. 1993. Spiders in Ecological Webs. Cambridge University Press, Cambridge.

I-Min Tso[1] and **Lucia Liu Severinghaus**: Institute of Zoology, Academia Sinica, Nankang, Taipei 11529, Taiwan

[1]*Current address:* Dept. of Biology, Tunghai University, Taichung 407, Taiwan.

JOSEPH C. CHAMBERLIN
(1898–1962)

A Tribute To
Joseph C. Chamberlin
on the occasion of the
100th anniversary of his birth
23 December 1898

arranged by

Mark S. Harvey
Western Australian Museum, Francis Street,
Perth, Western Australia 6000, Australia

and

Mark Judson
Muséum national d'Historie naturelle,
Laboratoire de Zoologie (Arthropodes), 61 rue de Buffon,
75005 Paris, France

PREFACE

He who would study the false scorpions, either biologically or morphologically, will find his reward in the fascination of the bizarre and the little known, for indeed they constitute one of the most peculiar and one of the lesser known groups of animals. Small and harmless enough not to excite fear or repugnance; obscure and drab enough not to have attracted the attention of the "stamp-collecting" type of naturalist; rare enough to give pleasure in collecting; small enough to require the development of a considerable degree of skill in their preparation for study; numerous enough in point of history to throw light upon many problems of distribution—these are features that invest the false scorpions with a genuine interest.

Joseph Conrad Chamberlin
(1931, *The Arachnid Order Chelonethida*, p. 6)

Despite their small size and inconspicuous nature, pseudoscorpions have occupied the minds of naturalists since Aristotle. However, early accounts failed to recognize their unique features, and indeed Linnaeus grouped the two species he recognized along with harvestmen and other distantly related arachnids in the genus *Phalangium*. Many European taxonomists of the 19th century, including the great arachnologists Carl L. Koch, Ludwig Koch and Eu-

gène Simon, made significant contributions to pseudoscorpion taxonomy, which were soon followed by others, including Luigi Balzan, Hans Hansen and Carl With, all of whom published insightful observations on the classification of the group.

However, it was not until the late 1920's that the classification of pseudoscorpions came under critical study again, by a taxonomist who had been trained under the watch-

ful eye of Gordon F. Ferris at Stanford University, California. By 1931, Joseph Conrad Chamberlin (1898–1962) had already published two major taxonomic synopses, as well as an exceptional synthesis on their morphology and biology that remains a benchmark against which all later papers must be judged. 'The Arachnid Order Chelonethida' (published by Stanford University Press in 1931) quickly became the standard reference work for all pseudoscorpion workers, containing numerous detailed and meticulously illustrated observations of virtually all aspects of pseudoscorpion morphology, a novel classificatory system and a review of pseudoscorpion biology. Chamberlin's systematic framework included the recognition and naming of many new taxa, including several ordinal-group names (the Groups Heterosphyronida and Homosphyronida, and the Suborders Heterosphyronida, Diplosphyronida and Monosphyronida), and numerous new family-group, genus-group and species-group names. His classification was quickly adopted with little modification by Max Beier in 1932, working in the Naturhistorisches Museum, Vienna, whose monographic treatment of the world fauna, published in *Das Tierreich,* represents another landmark in the study of pseudoscorpions.

Although no fossils older than the Oligocene had been found when Chamberlin wrote the prescient paragraph quoted above, pseudoscorpions are an ancient group which date back to the Devonian, making them one of the oldest orders of organisms still alive today. Also, he could not have known that within 60 years of his major contributions to the study of pseudoscorpions, over 3000 species in 440 genera would be described from around the world—a far cry from the 800 or so species known by 1931.   However, it is not only with regard to the taxonomy and classification of the group that we should be grateful to him,

since his numerous observations on diverse aspects of their morphology and biology are fitting testimony to his acute powers of deduction.

As a small token of the high regard in which Joseph Chamberlin is held by his fellow pseudoscorpion taxonomists, two genus-group names and 11 species have been named in his honor. These are listed in chronological order in their current combination: *Apocheiridium (Apocheiridium) chamberlini* Godfrey 1927; *Fissilicreagris chamberlini* (Beier 1931); *Afrosternophorus chamberlini* (Redikorzev 1938); *Haploditha chamberlinorum* Caporiacco 1951 (named for Chamberlin and his uncle, Ralph V. Chamberlin); *Kleptochthonius (Chamberlinochthonius)* Vachon 1952; *Pararoncus chamberlini* (Morikawa 1957); *Larca chamberlini* Benedict & Malcolm 1978; *Cheiridium chamberlini* Dumitresco & Orghidan 1981; *Chthonius (Chthonius) chamberlini* (Leclerc 1983); *Chamberlinarius* Heurtault 1990; *Hya chamberlini* Harvey 1993; *Tyrannochthonius chamberlini* Muchmore 1996; *Anysrius chamberlini* Harvey (this volume) and *Rhopalochernes chamberlini* Heurtault (this volume).

The purpose of the present tribute, in which we have brought together several scientific papers, along with a biography of J.C. Chamberlin, is to acknowledge the immense contribution that Joseph Conrad Chamberlin has made to the study of pseudoscorpions. December 23, 1998 marks the 100th anniversary of the birth of an exceptional arachnologist, whose foresight and keen eye have left us a published legacy which will continue well into the next millennium.

We wish to thank the Executive Board of the American Arachnological Society, and especially Jim Berry and Petra Sierwald, who have made this tribute possible.

Mark S. Harvey: Western Australian Museum, Perth

JOSEPH C. CHAMBERLIN
1898–1962

Joseph Conrad Chamberlin was born in Salt Lake City, Utah, on 23 December 1898, the first child of Ole and Mary Ethel (Conrad) Chamberlin. Both of his parents were descended from early Mormon pioneer families. His father's ancestry was mainly English, while his mother's family had English and German roots.

His father died in 1911, leaving the family nearly destitute. Being the eldest child in the family, Joseph had great responsibilities placed on him to help support the family and assist in the care of his brothers, Philip and Ole Wilbert, and sister, Dorothy. In 1914, after completing only a year of high school, he left school in order to supplement his mother's modest salary. For the next three and a half years, he worked as a sheep herder and camp tender on his uncle's large sheep ranges, and as a repairman and tester for a local company making the radios of the day.

In October 1918, just before the end of the First World War, Chamberlin was drafted into the U.S. Army. Shortly afterwards, he was stricken by the terrible influenza epidemic that swept through the United States that year. This developed into pneumonia, at which point almost all hope for his life was abandoned. With so many men sick and dying and so few doctors, all that could be done for most of the patients was to make them comfortable and leave them to die. However, a nurse took an interest in Chamberlin and persuaded the doctors to help him. His most serious problem was a condition (empyema) affecting his left lung. The treatment at the time was to remove a rib closest to the affected lung in order to collapse it. Despite the severe pain and trauma of the surgery (he was too weak to be given an anesthetic), he slowly began to improve, and finally recovered.

After the end of the war, Congress passed legislation allowing veterans to receive a year of free tuition at an accredited school, to help them return to civilian life. In the fall of 1919, Chamberlin enrolled at the University of Utah, taking preliminary courses in mechanical en-

Joseph C. Chamberlin
Palo Alto, 1928

gineering. Although he had been seriously interested in pursuing a career in the biological sciences for quite some time, the family's circumstances led him to choose what seemed to be the quickest and most practical way to gain a profession.

When Congress voted to revise the previous legislation and allow veterans to obtain a full four years of schooling for an academic degree, Chamberlin's uncle—the arachnologist Ralph Vary Chamberlin—counseled him to apply for a transfer to Stanford University to study Entomology. Although he only had about a year of high school, the usual entrance requirements were waived because of his status as a veteran and he was accepted as a "Special Student" in the Department of Zoology, majoring in Entomology.

At Stanford, he soon came under the tutelage of Prof. Gordon Floyd Ferris, who was to become a lifelong friend. Although only five years older than Chamberlin, Ferris al-

ready had an international reputation as an entomologist. The two men had similar backgrounds and shared much the same outlook on science. Ferris trained Chamberlin as a systematic entomologist, describing him as "an excellent student, one of the best that we have had here for many years." The most obvious sign of Ferris' influence can be seen in the development of his drawing technique. Chamberlin was soon producing illustrations with a combination of artistry and accuracy that has never been rivaled for pseudoscorpions. Ferris' influence did not, however, sway Chamberlin from his early passion for these endearing animals.

"My interest in the false scorpions dates from a chance encounter with one while still a school boy in my home town of Salt Lake City, Utah. I was busily engaged in creating a miniature zoo of backyard jungle denizens—complete with pill box cages provided with close set pins in lieu of bars. Among the candidates for this zoological garden was a queer flattened tick-like creature with enormous crab-like claws which it handled as dexterously as a boxer his gloved fists which, to my unaided eye, they resembled.

I made a number of penciled sketches of this mysterious 'boxing bug' showing its various stances. It possessed an enormous fascination for me, what with its sudden alerts, its tentative advances, and precipitate retreats. I never forgot it, in spite of the fact that it was years before I saw another representative—this time as a sophomore student in entomology at Stanford University in the fall of 1920. My interest—and memory—immediately revived, and now with books and microscope at hand I was able to identify my mysterious 'boxing animal' as a pseudoscorpion. That was the spark, and with an inspiring teacher at hand in the person of Gordon Floyd Ferris, I was encouraged to find out 'everything I could' about these little arachnids. . ." (J.C. Chamberlin, unpubl. manuscript).

After having been at Stanford for only a year, he was invited to take part in the California Academy of Science Expedition to the Gulf of California, which lasted 87 days (April 17–July 10, 1921) and sailed a total of

1811 miles (Slevin 1923). This was quite an honor, since such invitations were usually only given to promising graduate students. Although nominally assistant to the entomologist, P. Van Duzee, during the expedition, Chamberlin was given much latitude to pursue his own interests. He collected a wide range of groups, reflected in the species named after him (e.g., *Bulimulus chamberlini* Hanna (Gasteropoda), *Centrioptera chamberlini* Blaisdell (Tenebrionidae), *Ticida chamberlini* Van Duzee (Hemiptera), *Evagrus josephus* R.V. Chamberlin (Araneae) and *Euphorbia chamberlini* Johnston). Naturally, he also found a large number of new pseudoscorpions, including the first known specimens of the remarkable family Menthidae Chamberlin.

In 1923, he obtained his B.A. degree in Entomology "with distinction" and published an important monograph of the lac insects (Coccidae). The following year, he graduated as an M.A., again in Entomology. The subject of his master's thesis was originally "The application of graphical methods to a study of systematic biology, particularly systematic entomology," but this proved to be too broad and was changed to "A revision of the higher classification of the arachnid order Pseudoscorpionida, as based primarily upon a collection from the British Museum of Natural History." From 1924–26, he was an Entomology Assistant at the University of California Citrus Experimental Station, located at Riverside, California. During 1926 to 1928, he was an Instructor in General Biology at San Jose State Teachers College (now San Jose State College) in California, where he taught botany and other courses in biology, including one on the entomology of subtropical fruits. Chamberlin put a great deal of enthusiasm and vitality into his teaching and was much appreciated by his students. For a brief period (1927–1928), he worked as a part-time Special Investigator on the physiological effects of certain chemical sprays on living plants for the California Spray-Chemical Company, San Jose, California.

In 1929, he received his Ph.D. from Stanford University. His thesis was published in two parts. The first part was a series of systematic papers (1929–1930), in which the classification of the order was redefined and a large number of new taxa were described at all levels. The second part was his famous

monographic study of the comparative morphology of pseudoscorpions, entitled *The Arachnid Order Chelonethida*. Although completed soon after the systematic papers, problems at Stanford University Press caused a two-year delay in its publication. However, once published, this work radically changed the way in which pseudoscorpions were studied. Its pages are filled with original insights, abundantly illustrated with high-quality drawings. It has inspired all subsequent students, and is still the standard reference on the morphology and evolution of the order.

The classification that resulted from these studies remained largely unchallenged for over half a century. It was not until the publication of Harvey's (1992) cladistic analysis that an alternative was proposed. The durability of Chamberlin's classification is due not only to the quality of his work, but also to his remarkably modern outlook on systematics. Indeed, Chamberlin was one of the first to argue for what we would now call a phylogenetic (Hennigian) classification.

In an unpublished manuscript, quoted at length by Ferris (1928), Chamberlin argued that speciation was fundamentally dichotomous and that each dichotomy in a phylogenetic system, whether it is named or not, is a group or category of species. Each dichotomy, in turn, is of equal rank: "One branch, for example, might contain its full quota of eight species, while its alternative branch might contain but one. On this basis the single species is genetically the equivalent of the other eight." These ideas were applied to his classifications of both lac insects (1923) and pseudoscorpions (1931), for which fully-dichotomous, branching diagrams were presented, with all taxa treated as terminal (non-ancestral). There is an exact correspondence between these diagrams and the classifications, with sister groups being given equivalent rank. The only element of modern cladistics missing from his work was the concept of synapomorphy, but even here, Chamberlin recognized that negative criteria should be avoided whenever possible, believing that phylogenetic unity was revealed by "positive morphological criteria." It is not known whether Chamberlin's ideas influenced the development of phylogenetic systematics, but it would be surprising if Hennig had never read

Ferris' (1928) *Principles of Systematic Entomology*.

By the time his monograph was published, Chamberlin had raised the number of recognized families in the order from five to eighteen. Anticipating criticism of "inordinate 'splitting,'" Chamberlin (1929) argued that the large number of new supraspecific taxa was justified by the fact that only a small proportion of the world's species was known. However, he also considered Chelonethi to be a very ancient group. Writing to Hirst, in 1922, about the discovery of arachnid fossils in the Rhynie chert, he said

> "I hope your material has not yet run out and that ultimately a pseudoscorpion may turn up in the same formation. I personally strongly incline to the belief that they must have existed at least as early as the middle Paleozoic. As you know there are no known pseudoscorpion remains from before the Oligocene (amber), and hence discovery of true Paleozoic remains would be a find of the first order. I certainly hope you are lucky enough to make it."

This remarkable prediction has been confirmed by the recent discovery of a Devonian fossil, which is very similar to modern groups (Schawaller et al. 1991).

In the same month that the monograph was completed, Chamberlin accepted a position with the U.S. Department of Agriculture in June 1929, as leader of the Beet Leafhopper Project at the Twin Falls Field Station, Idaho, becoming Chief of the station in 1932. This was followed by assignments to the field stations at Modesto, California (1935–1936) and Corvallis, Oregon (1936–39). In 1939, he moved to the Forest Grove Field Station, Oregon, where he was to spend the rest of his career, retiring as its Chief in 1961. From 1937–1943, he was head of the Pea Weevil Investigation and later of the Pea Insects Investigations, which were later broadened into a general study of insecticide application methods. This involved studying methods of applying insecticides from the air, a topic on which he was invited to speak at the Tenth International Congress of Entomology in Montreal, in 1956.

During the summers of 1943–1946, he was given a special assignment to study the insect

Joseph C. Chamberlin (left) and Gordon F. Ferris (right) at the 10th International Congress of Entomology, Montreal, Canada, 1956.

fauna of the Matanuska Valley in Alaska, in conjunction with the University of Alaska Experiment Station, located at Palmer, Alaska. Although Chamberlin's career as an economic entomologist was a distinguished one, he always regretted that his abilities as a teacher and researcher could not be utilized more directly. Unfortunately, systematic research was not a priority for the USDA and his requests to be transferred to a less applied bureau were to no avail.

Chamberlin was elected to membership of the Phi Beta Kappa and Sigma Xi fraternities in 1923; a Stanford University Fellow (1923–24); a Fellow of the American Association for the Advancement of Science in 1928; and a Fellow of the Entomological Society of America in 1938. He was also a member of the Oregon, Washington and Pacific Coast entomological societies, serving on the publications committee of the latter. In 1962, he received a citation from the Oregon Academy of Sciences for his "outstanding service to the field of Science."

On 26 May 1923, Chamberlin married Clara Hya Gladstone, a young Russian woman and recent emigrant to the United States. They had five children: Laura Anne (1924), Phyllis (1926), Mary Joan (1930), David Conrad (1932) and Alice Ruth (1937). The marriage ended in 1938, and six years later, in 1944, he married Mrs. Charlotte May (Guerdan) Young.

Despite his intellectual accomplishments, Chamberlin was a very down-to-earth and unassuming man, a congenial host, kind and generous to his friends and family, and possessed of great natural artistic gifts. As David Malcolm put it:

"Joe was a warm, kindly, extremely generous, and out-going man with a quick wit and a delightful sense of humor. He loved a good laugh. He loved life, his friends (who were many), and his work. . . He was meticulous and thoughtful in all he approached, a gentleman, an extremely productive scientist."

Apart from his work and family, Chamberlin had a great variety of interests. He had an encyclopedic knowledge of history, philosophy and the great literature. He was especially fond of reading poetry, and would often enliven conversations with recitations from

memory. If he had so chosen, he could probably have become an outstanding writer. Though he did not become seriously interested in photography until his mid-fifties, he quickly became an accomplished photographer, winning many awards in various Color Slide Salons of the Photographic Society of America and attaining the status of a three-star exhibitor. He also helped organize the Forest Grove Camera Club, where he was always willing to pass on his skills.

As the years passed, his career and other vicissitudes of life demanded an increasing share of his time, severely limiting his work on the false scorpions. His earlier systematic papers had been planned as preludes to generic revisions of the families, but only two of these, on the Tridenchthoniidae and Hyidae, were to appear. Another difficulty was that his later descriptions became increasingly detailed and time consuming.

In the late 1950s, Chamberlin met David Malcolm at a meeting of the Oregon Entomological Society. When Malcolm, who had recently completed a Ph.D. on phytophagous mites, expressed an interest in working on a different arachnid group, Chamberlin naturally asked whether he had considered pseudoscorpions and invited him to his lab in Forest Grove. This resulted in their collaboration on the cavernicolous northern American pseudoscorpions that had been accumulating in Chamberlin's collection, a subject that had been barely touched upon previously.

Beginning in the mid-1940s, Chamberlin started to experience the first symptoms of emphysema (a little-known disease at the time), which progressively worsened. The loss of function in his left lung in 1918, now became an overwhelmingly negative factor in the course of this disease. In February 1961, he was finally forced to take an early retirement from his position with the U.S. Department of Agriculture. A little more than a year later, on 17 July 1962, he died in a hospital in Hillsboro, Oregon, at the age of 63. His pseudoscorpion collection—the largest ever in private hands—passed to David Malcolm. This, together with Chamberlin's unpublished files and the collections of Malcolm and Ellen Benedict, has recently been deposited at the California Academy of Sciences.

In the preface to *The Arachnid Order Chelonethida*, Chamberlin expressed a hope that it would "furnish a base or starting point for the student of false scorpions similar to that afforded by the various manuals of other groups, among which we may specifically note Williston's *Manual of North American Diptera* and Comstock's *Spider Book.*" It did more than that. No other work on a major group of arachnids has defined its subject with the same clarity, conciseness and authority. Chamberlin's flair for the interpretation of characters and the recognition of natural groups has left an indelible mark; he deserves to be remembered as one of the great arachnologists.

ACKNOWLEDGMENT

Mark Judson
David C. Chamberlin

LITERATURE CITED
(other than by J.C. Chamberlin)

Ferris, G.F. 1928. The principles of systematic entomology. Stanford Univ. Publ., Univ. Ser. (Biol. Sci.), 5(3):101–269. [MS by J.C. Chamberlin quoted on pp. 219–222.]

Harvey, M.S. 1992. The phylogeny and classification of the Pseudoscorpionida (Chelicerata: Arachnida). Invert. Taxon., 6:1373–1435.

Schawaller, W., W.A. Shear & P.M. Bonamo. 1991. The first Paleozoic pseudoscorpions (Arachnida, Pseudoscorpionida). American Mus. Novit., 3009:1–17.

Slevin, J.R. 1923. Expedition of the California Academy of Sciences to the Gulf of California in 1921. General account. Proc. California Acad. Sci., (4) 12 [1922] (6):55–72, 1 map.

PUBLICATIONS BY J.C. CHAMBERLIN

General:
Chamberlin, J.C. 1924. Concerning the hollow curve of distribution. American Nat., 58:350–374.

Becking, L.B. & J.C. Chamberlin. 1925. A note on the refractive index of chitin. Proc. Soc. Exp. Biol. Med., 22:256–257.

Chamberlin, J.C. 1925. Heavy mineral oil as a permanent non-volatile preservative for valuable biological material. Science, 61 (1590):634–635.

Ferris, G.F. & J.C. Chamberlin. 1928. On the use of the word "chitinized." Entomol. News, 39: 212–215.

Chelonethida (false scorpions):

Chamberlin, J.C. 1921. Notes on the genus *Garypus* in North America (Pseudoscorpionida–Cheliferidae). Canadian Entomol., 53:186–191.

Chamberlin, J.C. 1923. The genus *Pseudogarypus* Ellingsen (Pseudoscorpionida–Feaellidae). Entomol. News, 34 (5):146–149; (6):161–166, pl. 5.

Chamberlin, J.C. 1923. New and little known pseudoscorpions, principally from the islands and adjacent shores of the Gulf of California. Proc. California Acad. Sci., (4) 12 (17) [1922]:353–387.

Chamberlin, J.C. 1923. On two species of pseudoscorpion from Chile with a note on one from Sumatra. Rev. Chilena Hist. Nat., 27:185–192.

Chamberlin, J.C. 1924. Preliminary note upon the pseudoscorpions as a venomous order of the Arachnida. Entomol. News, 35:205–209.

Chamberlin, J.C. 1924. The Cheiridiinae of North America (Arachnida–Pseudoscorpionida). Pan-Pacific Entomol., 1 (1):32–40.

Chamberlin, J.C. 1924. Giant *Garypus* of the Gulf of California. Nature Mag. (Washington, D.C.), 2 (Sept.):171–172, 175.

Chamberlin, J.C. 1924. *Hesperochernes laurae,* a new species of false scorpion from California inhabiting the nest of *Vespa.* Pan-Pacific Entomol., 1 (2):89–92.

Chamberlin, J.C. 1925. On a collection of pseudoscorpions from the stomach contents of toads. Univ. California Publ. Entomol., 3 (4):327–332.

Chamberlin, J.C. 1926. Papers from Dr. Th. Mortensen's Pacific Expedition, 1914–16. XXXVI. Notes on the status of genera in the Chelonethid family Chthoniidae together with a description of a new genus and species from New Zealand. Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn, 81:333–338.

Chamberlin, J.C. 1929. *Dasychernes inquilinus* from the nest of meliponine bees in Colombia (Arachnida: Chelonethida). Entomol. News, 40:49–51.

Chamberlin, J.C. 1929. *Dinocheirus tenoch,* an hitherto undescribed genus and species of false scorpion from Mexico (Arachnida–Chelonethida). Pan-Pacific Entomol., 5 (4):171–173.

Chamberlin, J.C. 1929. The genus *Pseudochthonius* Balzan (Arachnida–Chelonethida). Bull. Soc. Zool. France, 54 (3):173–179.

Chamberlin, J.C. 1929. A synoptic classification of the false scorpions or chela-spinners, with a report on a cosmopolitan collection of the same. – Part 1. The Heterosphyronida (Chthoniidae) (Arachnida–Chelonethida). Ann. Mag. Nat. Hist., (10) 4:50–80.

Chamberlin, J.C. 1929. On some false scorpions of the suborder Heterosphyronida (Arachnida–Chelonethida). Canadian Entomol., 61:152–155.

Chamberlin, J.C. 1929. The comparative morphology of the arachnid order Chelonethida. Stanford Univ. Bull., (5) 78 [Abstracts of dissertations, Stanford Univ. 1928–1929, vol. 4]:25–27.

Chamberlin, J.C. 1930. A synoptic classification of the false scorpions or chela-spinners, with a report on a cosmopolitan collection of the same. – Part II. The Diplosphyronida (Arachnida–Chelonethida). Ann. Mag. Nat. Hist., (10) 5:1–48, 585–620.

Chamberlin, J.C. 1931. *Parachernes ronnaii,* a new genus and species of false scorpion from Brazil (Arachnida–Chelonethida). Entomol. News, 42:192–195.

Chamberlin, J.C. 1931. The arachnid order Chelonethida. Stanford Univ. Publ., Univ. Ser., (Biol. Sci.) 7(1):1–284.

Chamberlin, J.C. 1931–32. A synoptic revision of the generic classification of the chelonethid family Cheliferidae Simon. (Arachnida). Canadian Entomol., 63 [1931]:289–294; 64 [1932]:17–21, 35–39.

Chamberlin, J.C. 1932. On some false scorpions of the superfamily Cheiridioidea (Arachnida, Chelonethida). Pan-Pacific Entomol., 8 (3):137–144.

Chamberlin, J.C. 1933. Some false scorpions of the atemnid subfamily Miratemninae. (Arachnida–Chelonethida.). Ann. Entomol. Soc. America, 26 (2):262–268, pl. 1.

Chamberlin, J.C. 1934. On two species of false scorpions collected by birds in Montana, with notes on the genus *Dinocheirus* (Arachnida–Chelonethida). Pan-Pacific Entomol., 10 (3):125–132.

Chamberlin, J.C. 1934. Check list of the false scorpions of Oceania. Occ. Pap. B.P. Bishop Mus., 10 (22):1–14.

Chamberlin, J.C. 1935. A new species of false scorpion (*Hesperochernes*) from a bird's nest in Montana. Pan-Pacific Entomol., 11 (1):37–39.

Chamberlin, J.C. 1935. Chelonethida. Pp. 477–481. *In* A Manual of the Common Invertebrate Animals (Exclusive of Insects) (H.S. Pratt, ed.). Blakiston: Philadelphia.

Chamberlin, J.C. 1938. A new genus and three new species of false scorpion from Yucatan Caves (Arachnida–Chelonethida). Publ. Carnegie Inst., Washington, 491:109–121.

Chamberlin, J.C. 1938. New and little-known false-scorpions from the Pacific and elsewhere. (Arachnida–Chelonethida.) Ann. Mag. Nat. Hist., (11) 2:259–285.

Chamberlin, J.C. 1939. Tahitian and other records of *Haplochernes funafutensis* (With) (Arachnida: Chelonethida). Bull. B.P. Bishop Mus., 142:203–205.

Chamberlin, J.C. 1939. New and little-known false scorpions from the Marquesas Islands (Arachnida: Chelonethida). Bull. B.P. Bishop Mus., 142:207–215.

Chamberlin, J.C. 1943. The taxonomy of the false

scorpion genus *Synsphyronus,* with remarks on the sporadic loss of stability in generally constant morphological characters (Arachnida: Chelonethida). Ann. Entomol. Soc. America, 36 (3): 486–500.

Chamberlin, J.C. & R.V. Chamberlin. 1945. The genera and species of the Tridenchthoniidae (Dithidae), a family of the arachnid order Chelonethida. Bull. Univ. Utah, 35 (23) (Biol. Ser., 9 (2)):1–67.

Chamberlin, J.C. 1946. The genera and species of the Hyidae, a family of the arachnid order Chelonethida. Bull. Univ. Utah, 37 (6) (Biol. Ser., 9 (6)):1–16.

Chamberlin, J.C. 1947. Three new species of false scorpions from the island of Guam (Arachnida, Chelonethida). Occ. Pap. B.P. Bishop Mus., 18 (20):305–316.

Chamberlin, J.C. 1947. The Vachoniidae, a new family of false scorpions represented by two new species from caves in Yucatan (Arachnida, Chelonethida, Neobisioidea). Bull. Univ. Utah, 38 (7) (Biol. Ser. 10 (4)):1–15.

Chamberlin, J.C. 1949. New and little-known false scorpions from various parts of the world (Arachnida, Chelonethida), with notes on structural abnormalities in two species. American Mus. Novit., 1430:1–57.

Chamberlin, J.C. 1952. New and little-known false scorpions (Arachnida, Chelonethida) from Monterey County, California. Bull. American Mus. Nat. Hist., 99:259–312.

Malcolm, D.R. & J.C. Chamberlin. 1960. The pseudoscorpion genus *Chitrella* (Chelonethida, Syarinidae). American Mus. Novit., 1989:1–19.

Chamberlin, J.C. & D.R. Malcolm. 1960. The occurrence of false scorpions in caves with special reference to cavernicolous adaptation and to cave species in the North American fauna. (Arachnida–Chelonethida.) American Midl. Nat., 64 (1): 105–115.

Malcolm, D.R. & J.C. Chamberlin. 1961. The pseudoscorpion genus *Kleptochthonius* Chamberlin (Chelonethida, Chthoniidae). American Mus. Novit., 2063:1–35.

Chamberlin, J.C. 1962. New and little-known false scorpions, principally from caves, belonging to the families Chthoniidae and Neobisiidae (Arachnida, Chelonethida). Bull. American Mus. Nat. Hist., 123:303–352.

Muchmore, W.B. & J.C. Chamberlin. 1995. The genus *Tyrannochthonius* in the eastern United States (Pseudoscorpionida: Chthoniidae). Part I. The historical taxa. Insecta Mundi, 9 (3–4):249–257.

Crustacea:
Chamberlin, J.C. & C.D. Duncan. 1924. Notes on *Lepidurus glacialis* Kroyer Crustacea, Brachi-

poda, Apodidae. J. Entomol. Zool., Pomona College, 16:99–105, pls. 1, 2.

Systematic entomology:
Chamberlin, J.C. 1923. A revision of the genus *Anisembia,* with description of a new species from the Gulf of California. Proc. California Acad. Sci., (4) 12 [1922] (16):341–351.

Chamberlin, J.C. 1923. A systematic monograph of the Tachardiinae or lac insects (Coccidae). Bull. Entomol. Res., 14 (2):147–212, pls. 10–20.

Chamberlin, J.C. 1925. Supplement to a monograph of the Lacciferidae (Tachardiinae) or lac insects (Homopt., Coccidae). Bull. Entomol. Res., 16 (1):31–41.

Chamberlin, J.C. 1925. A new species of *Lepidosaphes* from China (Hemiptera, Coccidae). Pan-Pacific Entomol., 2 (2):85–87.

Chamberlin, J.C. 1927. Status and synonymy of the dictyospermum scale. Monthly Bull. California State Dept. Agric., 14 (9):484–491.

Chamberlin, J.C. & G.F. Ferris. 1929. On *Liparocephalus* and allied genera (Coleoptera; Staphylinidae). Pan-Pacific Entomol., 5 (3):137–143; (4):153–162.

Economic entomology:
deOng, E.R., H. Knight & J.C. Chamberlin. 1927. A preliminary study of petroleum oil as an insecticide for citrus trees. Hilgardia, 2 (9):351–385.

Knight, H., J.C. Chamberlin & C.D. Samuels. 1929. On some limiting factors in the use of saturated petroleum oils as insecticides. J. Plant Physiol., 4:299–321.

Fulton, R.A. & J.C. Chamberlin. 1931. A new automatic insect trap for the study of insect dispersion and flight associations. J. Econ. Entomol., 24 (3):757–761, pl. 25.

Annand, P.N., J.C. Chamberlin, C.F. Henderson & H.A. Waters. 1932. Movements of the beet leaf hopper in 1930 in southern Idaho. U.S. Dept. Agric. Circular, 244, 24 pp., figs.

Fulton, R.A. & J.C. Chamberlin. 1934. An improved technique for the artificial feeding of the beet leafhopper with notes on its ability to synthesize glycerides. Science, 79 (April 13):346–348.

Piemeisel, R.L. & J.C. Chamberlin. 1936. Land improvement measures in relation to a possible control of the beet leafhopper and curly top. U.S. Dept. Agric. Circular, 416, 25 pp.

Chamberlin, J.C. & K.W. Gray. 1938. Suggestions for the control of the pea weevil in Oregon with special reference to peas grown for processing. Oregon State Coll. Exp. Stn. Circular, 126:23 pp.

Chamberlin, J.C. & F.R. Lawson. 1940. A mechanical trap for the sampling of aerial insect populations. U.S. Dept. Agric., Bur. Entomol. & Pl. Quar., ET–163:12 pp.

Chamberlin, J.C. & F.R. Lawson. 1945. A me-
    chanical trap for the sampling of aerial insect
    populations. Mosquito News, 5 (1):4–7.
Fox, D.E., J.C. Chamberlin & J.R. Douglass. 1945.
    Factors affecting curly top damage to sugar beets
    in southern Idaho. U.S. Dept. Agric. Tech. Bull.,
    897:29 pp.
Stage, H.H. & J.C. Chamberlin. 1945. Abundance
    and flight habits of certain Alaskan mosquitoes
    as determined by means of a rotary-type trap.
    Mosquito News, 5 (1):8–16.
Brindley, T.A., J.C. Chamberlin, F. Hinman & K.W.
    Gray. 1946. The pea weevil and methods for its
    control. U.S. Dept. Agric. Farmers' Bull., 1971:
    1–24. (Revised in 1952, under authorship of T.A.
    Brindley, J.C. Chamberlin & R. Schopp).
Chamberlin, J.C. 1949. Insects of agricultural and
    household importance in Alaska. Univ. Alaska
    Bull., Agr. Expt. Stn. Circular, 9:59 pp.
Lawson, F.R., J.C. Chamberlin & G.T. York. 1951.
    Dissemination of the beet leafhopper. U.S. Dept.
    Agric. Tech. Bull., 1030:59 pp.
Brindley, T.A. & J.C. Chamberlin. 1952. The pea
    weevil. U.S. Dept. Agric. Yearbook Agric., 1952:
    530–537.
Chamberlin, J.C. 1953. Characteristics of airplane
    spray patterns at low flight elevations. Proc. 9th
    Ann. North Central Weed Control Conf., Win-
    nipeg, Canada, 1952:42–43.
Chamberlin, J.C., C.W. Getzendaner, H.H. Hessig
    & V.D. Young. 1955. Studies of airplane spray-
    deposit patterns at low flight levels. U.S. Dept.
    Agric. Tech. Bull., 1110:45 pp.
Chamberlin, J.C. & V.D. Young. 1956. Insecticide
    applications with aircraft and ground rigs. Farm
    Chemicals, (December):50–53.
Young, V.D., J.C. Chamberlin, C.W. Getzendaner &
    C.E. Deonier. 1957. Improved row-crop sprayer
    and duster for potatoes and other row crops. U.S.
    Dept. Agric. Res. Service Mimeogr. Bull., ARS
    42 - 10:14 pp.
Chamberlin, J.C. & V.D. Young. 1958. Insecticide
    applications with aircraft and ground rigs. Proc.
    10th Int. Congr. Entomol., Montreal, 1956, 3:
    255–260.
Young, V.D., J.C. Chamberlin, C.W. Getzendaner &
    C.E. Deonier. 1958. An atomizing nozzle as-
    sembly for use with improved row-crop sprayer
    and duster for potatoes and other row crops. U.S.
    Dept. Agric. Res. Service Mimeogr. Bull., ARS
    42 - 10 (supplement):7 pp.
Chamberlin, J.C. 1959. Thomas Roscoe Chamber-
    lin, Sr. 1889–1958. J. Econ. Entomol., 52 (1):
    181–182.

A STERNOPHORID PSEUDOSCORPION (CHELONETHI) IN DOMINICAN AMBER, WITH REMARKS ON THE FAMILY

Mark L. I. Judson: Muséum national d'Histoire naturelle, Laboratoire de Zoologie (Arthropodes), 61 rue de Buffon, 75005 Paris, France

ABSTRACT.   The first known fossil of the pseudoscorpion family Sternophoridae is described from Dominican amber. The specimen, an adult female, is tentatively assigned to the extant species *Idiogaryops pumilus* (Hoff), known from Florida and Little Cayman Island. The incomplete state of the fossil is probably the result of scavenging while the animal was trapped on the surface of the resin. The cuticular parts have collapsed during fossilization and the golden appearance of the fossil is due to light being reflected from the surface of the cast, rather than from the cuticle itself. A thin layer of ceroteugument is recorded in Sternophoridae. The morphology of the coxal area is reinterpreted. The so-called pseudosternum is delimited by the apparent internal borders of the coxae, which have moved laterally. A Y-shaped canal runs from the openings of the coxal glands to the oral cavity, carrying their secretions, together with those of the accessory glands of the coxae, to the oral cavity. The canal is covered by a series of overlapping tecta on coxae I–III and posteriorly on the palpcoxae. The coxae are fused medially from the posterior margin of coxa I to the anterior margin of coxa IV. The internal modifications of the median and posterior maxillary lyrifissures of pseudoscorpions are shown to be apodemes of trochanteral muscles of the palp. The suboral setae of the manducatory process of certain Sternophoridae are vestigial, suggesting that they may be undergoing a regression. The parallel between the morphology of the vestitural setae and that of setae *b* and *sb* of the chelicera is used to identify the missing seta of Sternophoridae as *sb*.

The Sternophoridae are a small, homogeneous family of pseudoscorpions, strongly adapted for life under the bark of trees. The twenty described species are currently placed in three genera: *Garyops* Banks 1909 from North and Central America and the Caribbean; *Idiogaryops* Hoff 1963 from Florida and the Caribbean; and *Afrosternophorus* Beier 1967 from eastern Africa, India, Nepal, Sri Lanka, Southeast Asia and Australasia (Harvey 1985).

Given their ecology and distribution, it is not unexpected to find a member of the Sternophoridae in Dominican amber, which is relatively young (15–20 My; Iturralde-Vinent & MacPhee 1996). Schawaller (1980a, 1980b, 1981a, 1981b) recorded six pseudoscorpion genera from this fauna, all of which are represented by extant species in the Caribbean region or Central America. What is, perhaps, surprising is that the fossil described here is morphologically indistinguishable from *Idiogaryops pumilus* (Hoff 1963), a Recent species known from Florida and Little Cayman Island (Harvey 1985). The assignment of fossils to extant species is almost always ques-

tionable, if only because fewer of their characters are visible. However, there is no reason, other than age, to suppose that the present fossil belongs to a different species. Pseudoscorpions are known to be an ancient group (Schawaller et al. 1991) and the wide distribution and morphological homogeneity of Sternophoridae (Chamberlin 1932; Harvey 1985) suggest conservative rates of evolution within the family. Recent material of the three sternophorid genera has also been examined for comparative purposes and some of the results are given at the end of this paper.

Idiogaryops pumilus (Hoff)
(Figs. 1, 2)

Garyops depressa (not Banks): Banks 1909: 305–306; Hounsome 1980: 85 (in part: misidentifications).

Garyops pumila Hoff 1963: 7–10, figs. 5–6.

Idiogaryops pumilus (Hoff): Harvey 1985: 165–166, figs. 32, 38, 40, 46–50, map 2.

? *Idiogaryops* sp. Harvey 1985: 166–167, figs. 33, 40.

Material examined.—1 ♀, amber fossil (Miocene?) from Dominican Republic (exact provenance unknown). Deposited in the Nat-

Figure 1.—*Idiogaryops pumilus* (Hoff), female, dorsal view of amber fossil (image of left palp distorted by oblique edge of block).

ural History Museum, London (Dept. of Palaeontology; registration number JA 43). Presented by R. Rontaler, 5 December 1996. The amber piece is clear, golden-yellow and has been ground and polished parallel to the dorsal plane of the specimen to facilitate accurate observations.

Description of fossil.—Palps and anterior part of carapace deep reddish-brown; legs and posterior region of carapace yellowish-brown (probably darkened by process of fossilization). Vestitural setae of dorsal surfaces with blunt tips. Cuticular parts smooth, apart from granulation on lateral surfaces of palps. Most parts of body covered by a thin, clear layer of cerotegument, which seems to have expanded into the resin.

Carapace strongly flattened, with a moderate, lateral constriction at level of leg I; posterior part weakly sclerotized; surface with irregular transverse lines in anterior half; posterior margin lost. Eyes absent. Setae small and sparse. Pleural membrane finely plicate (portion visible on right side). Opisthosoma missing, only represented by cerotegument of ventral surface and a few detached setae.

Chelicerae with 4 setae on hand, *b* blunt, other setae acuminate. Spinneret difficult to see clearly, but apparently long and with three rami.

Palps as shown in Fig. 2. Femur and patella fairly robust; lateral surfaces with strong granulation, dorsal and ventral surfaces smooth. Femur with a long tactile seta, proximad of middle. Chela with granulation at base of hand; hand broader than deep, with sides subparallel in dorsal view and parallel in lateral view. Fixed finger with 7 trichobothria (*isb* absent). Movable finger with three trichobothria; *st* about one-third of distance from *b* to *t*. Fixed finger with 4 and movable finger with 6 thickened (presumably spatulate) setae on paraxial face. Distal teeth retrorse, proximal teeth reduced.

Coxae with 'pseudosternum' typical of family. Legs short and robust; arolia fan-shaped, shorter than the claws, which are robust. Setae (including 'tactile setae') typical. Joint between femur and patella of all legs vertical (slightly oblique dorsally) and immobile.
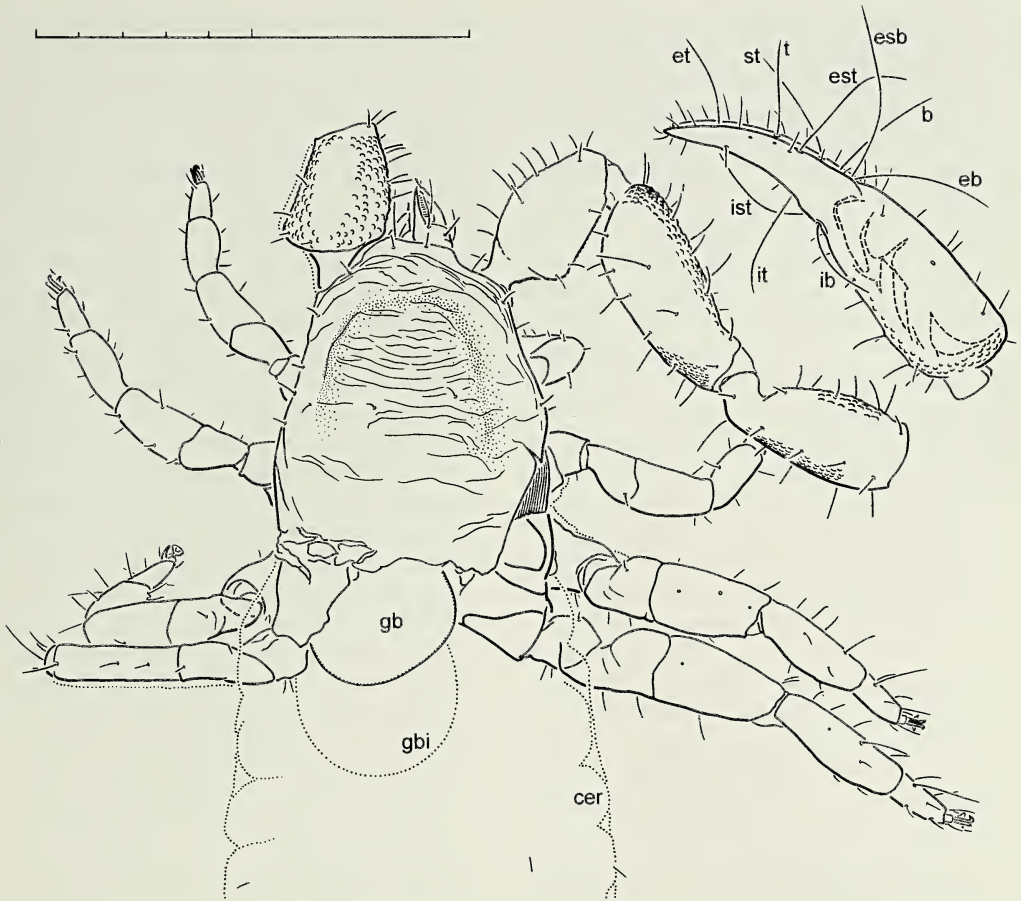
Measurements (in mm; ratios in parenthe-

Figure 2.—*Idiogaryops pumilus* (Hoff), female, dorsal view of fossil cast. Left palp omitted, apart from trochanter. Right chela shown separate from rest of palp simply for reasons of format (see Fig. 1 for true position). Cerotegument indicated by dotted lines (only shown in part). Cracking of cuticle only indicated on hand of chela. Granulation of palps only shown in part. Abbreviations: *cer* = cerotegument; *gb* = gas bubble; *gbi* = imprint of bubble in cerotegument. Scale line = 1 mm.

ses): Carapace (estimated) 0.84 × 0.61 (1.4). Right palp: trochanter 0.41 × 0.20 (2.05), 'heel' 0.29 (1.48); femur 0.59 × 0.20 (2.95); patella 0.46 × 0.20 (2.31); chela (including pedicel) 0.95 × 0.23 (4.10) length without pedicel 0.93 (4.04); hand length (with pedicel) 0.54 (2.34), without pedicel 0.51 (2.21), depth 0.18; movable finger 0.47 (0.97 length of hand without pedicel). Leg IV: femur 0.24 × 0.19 (1.3), patella 0.31 × 0.19 (1.6); femoropatella length 0.51 (2.7).

Remarks.—The fossil is almost indistinguishable from the descriptions of *I. pumilus* given by Hoff (1963) and Harvey (1985). The measurements of the palpal segments fall slightly below those given for Recent *I. pumilus* (e.g., femur length 0.62–0.72, patella

length 0.52–0.61, chela length without pedicel 0.95–1.07), but these differences are judged to be insignificant; the measurements of Recent specimens are based on only five females from Florida and are unlikely to represent the true range of variation in this species. It is also possible that the specimen has undergone some compression during fossilization (see remarks under Taphonomy).

Harvey (1985) briefly described and figured a male paratype of *I. pumilus* that differed from the male holotype in having a greatly reduced dorsal apodeme of the genitalia. Harvey concluded that the paratype belonged to a new species, but did not name it due to the lack of sufficient material. In the absence of any further information, it seems more rea-

sonable to regard the small apodeme of the paratype as either an abnormality or part of the normal range of variation in *I. pumilus*. However, if Harvey's interpretation is correct, it would not be possible to assign the fossil described here to either *I. pumilus* or the unnamed species.

TAPHONOMY

At first sight, the remains of the pseudoscorpion seem to be in very good condition. When examined more closely, however, it becomes clear that the cuticle has collapsed in many parts, resulting in extensive cracking (this is only indicated for the hand of the chela in Fig. 2). Hence, what is really seen is the cast left in the resin before the specimen collapsed. Because they were embedded in the resin, the hairs of the setae and trichobothria remained in their original positions, giving the cast a very lifelike appearance. The collapse of the cuticle explains the shiny golden appearance seen in reflected light, which is also characteristic of other Dominican amber fossils. Where the cuticle is no longer in contact with the amber, the light is reflected from the surface of the cast, but where it is still in contact with the amber, it is seen as a drab patch. Fortunately, the cuticle only collapsed after the resin had hardened, leaving a faithful representation of the external surfaces. The resin was able to diffuse through the cerotegument before hardening and seems to have caused it to expand.

The incomplete nature of the fossil was initially rather puzzling. The loss of part of the left palp, the opisthosoma and part of the carapace almost certainly occurred after the animal had become trapped on the surface of the resin. This can be deduced from the fact that the outline of the ventral surfaces has been preserved in the form of the cerotegument and a few detached hairs. There are no signs of decay, and the specimen cannot be an exuvium because, in addition to being adult, remains of the internal tissues can be seen. The only plausible explanation is that the exposed parts were scavenged shortly after the pseudoscorpion became stuck in the resin. The scavenger—perhaps an insect—must have been relatively large: it bit through the left palp at the base of the patella and tore the opisthosoma from the prosoma, leaving the cerotegument stuck in the resin.

The absence of debris suggests that the specimen was only briefly exposed before being covered by a second flow of resin. The removal of the body left a concavity in the surface of the first flow, which trapped an air bubble (Fig. 3: *gb*) just behind the carapace. At this point, the specimen was upside-down in the resin: the pressure of the bubble created a large bulge in the layer of cerotegument above it (Fig. 3: *gbi*). Before the resin solidified, it was turned over, such that the remains of the pseudoscorpion were dorsal side up relative to gravity. The bubble slowly rose away from the cerotegument and came to rest just below the torn margin of the carapace. From the size of the impression left in the cerotegument, it can be seen that the bubble decreased in volume. This could be due to diffusion, contraction of the resin or compression, either alone or in combination.

Because the cuticle cracked, rather than simply disintegrating, it was probably subjected to a significant pressure after being buried. If so, the cast now observed must be smaller than the living animal. Grimaldi et al. (1994) discussed differences in the size of cuticular parts of insects and their casts in amber, but concluded that "Since it is unlikely that the cuticular surface would shrink, even during dehydration, it is more likely that the cast surface represents expansion of the amber, probably due to polymerization of the original resin." There is indeed a large difference in size for the specimens they illustrate, without any obvious damage to the cuticle, but the assumption that cuticle cannot shrink during fossilization is questionable. If, as Grimaldi et al. suggest, an expansion of the amber has occurred, the original cuticle ought to show a finer, less distorted preservation of detail than the cast. From their scanning electron micrographs (e.g., figs. 26, 27), it appears that the opposite is the case, indicating that the cuticle has shrunk. Baroni Urbani (1980) interpreted the damage seen in certain ant specimens in Dominican amber as due to shrinkage and collapse of the cuticle, probably as a result of heating (D. Schlee *in* Baroni Urbani 1980).

The possibility of changes in size during fossilization has not been considered in previous studies of amber pseudoscorpions. Although the differences are probably small, it is evident that caution is needed when comparing morphometric data for fossil and Re-

cent specimens. In identifying the present fossil as *I. pumilus*, I have assumed that its dimensions have decreased slightly. If it could be shown that a significant increase in size was involved, this identification would be incorrect.

MORPHOLOGICAL NOTES

The following notes are mainly based on two adults (1♂1♀) of an undescribed *Afrosternophorus* species—closely related to *A. hirsti* (Chamberlin 1932)—from Australia (Northern Territory, The Bark Hut, Arnhem Highway, under bark of *Eucalyptus* sp. 18 June 1984, M. Kotzman; MH 611.07–08; deposited in MNHN). Additional observations were made on type material of *Garyops sini* (Chamberlin 1923) and *Afrosternophorus cylindrimanus* (Beier 1951) housed in MNHN, and on specimens of *G. depressus* (1♀, Dominican Republic, Pedernales Prov., 10 km N. Cabo Rojo, beating thorn scrub, 22 August 1988, M.I. Ivie, T.K. Philips & K.A. Johnson; WM 7186) and *I. paludis* (Chamberlin 1932) (1♂2♀, U.S. Virgin Islands, St. John, Great Lameshur Bay, East shore, under bark, 14 June 1980, W.B. Muchmore; WM 5705).

Cerotegument.—A layer of cerotegument is present in Sternophoridae, but it is easily overlooked because it is thin and closely appressed to the surface of the epicuticle. It is most evident when it becomes damaged and detached, as can be seen in Harvey's (1985: fig. 7) scanning electron micrograph of the coxal region of *A. hirsti*. In transmitted light, the cerotegument is transparent and shows a very fine, irregular granulation. Harvey (1992) regarded the presence of cerotegument ("pseudoderm") as a synapomorphy of the Garypidae and Larcidae (Garypoidea), but it is more widespread, occurring sporadically in at least the Cheliferoidea (e.g., Mahnert 1985) and Feaelloidea (pers. obs.).

Coxal tecta.—The presence of a 'pseudosternum' has traditionally been considered one of the most characteristic features of the Sternophoridae. Chamberlin (1923, 1931) defined it as a secondary space between the coxae, resulting from a "partial mesal membranization of coxae I to IV." Harvey (1985) failed to find any indication of a membrane in *A. hirsti*, using scanning electron microscopy, and therefore interpreted the pseudosternum as a desclerotization of the coxae, rather than

a membranization. The difference between these interpretations may seem slight, but it reflects an apparent incongruity between the observations made using light and scanning electron microscopy. When Hoff's light micrographs (1963: figs. 1, 5) are compared with Harvey's scanning electron micrograph (1985: fig. 7), the difference is striking. The explanation lies in the presence of a previously overlooked series of plate-like expansions of the paraxial walls of the coxae, which are here termed the *coxal tecta*.

The tecta are present on coxae I–III and the posterior part of the palp coxae. Their extreme thinness (about 2 μm where they meet) means that they are almost transparent and difficult to observe in ordinary preparations. They are best seen in specimens cleared in lactic acid. The following description is mainly based on the material of *A.* aff. *hirsti*, but the general form seems to be the same in other sternophorids.

The tecta of each side extend past the midline, which means that they overlap. In the specimen shown in Fig. 3, the tecta of the right coxae pass beneath those of the left coxae. In addition to this transverse overlapping, the tecta overlap longitudinally, with the tectum of one coxa lying beneath that of the following coxa. The combination of these two types of overlapping results in three points at which four tecta are superimposed. The second of these points has been marked q on Fig. 5. At this point (looking ventrally), the external tectum is that of right coxa I, below which is the tectum of the right coxa I, followed by that of right coxa II and finally the tectum of left coxa II, which is nearest to the body. This can be represented more concisely by the sequence right I/left I/right II/left II, going from ventral to dorsal. Naturally, it is the posterolateral margins of tecta I and the anterolateral margins of tecta II that are involved at q.

The space between the coxae is therefore completely covered anteriad of coxa IV and would not normally be visible with scanning electron microscopy. In reflected light, the tecta give the 'pseudosternum' a slightly iridescent appearance, caused by diffraction effects.

When a sternophorid is examined in transmitted light, two sets of apparent borders are evident. The first and most obvious of these are the internal walls of the coxae (to which the leg muscles are attached). These borders
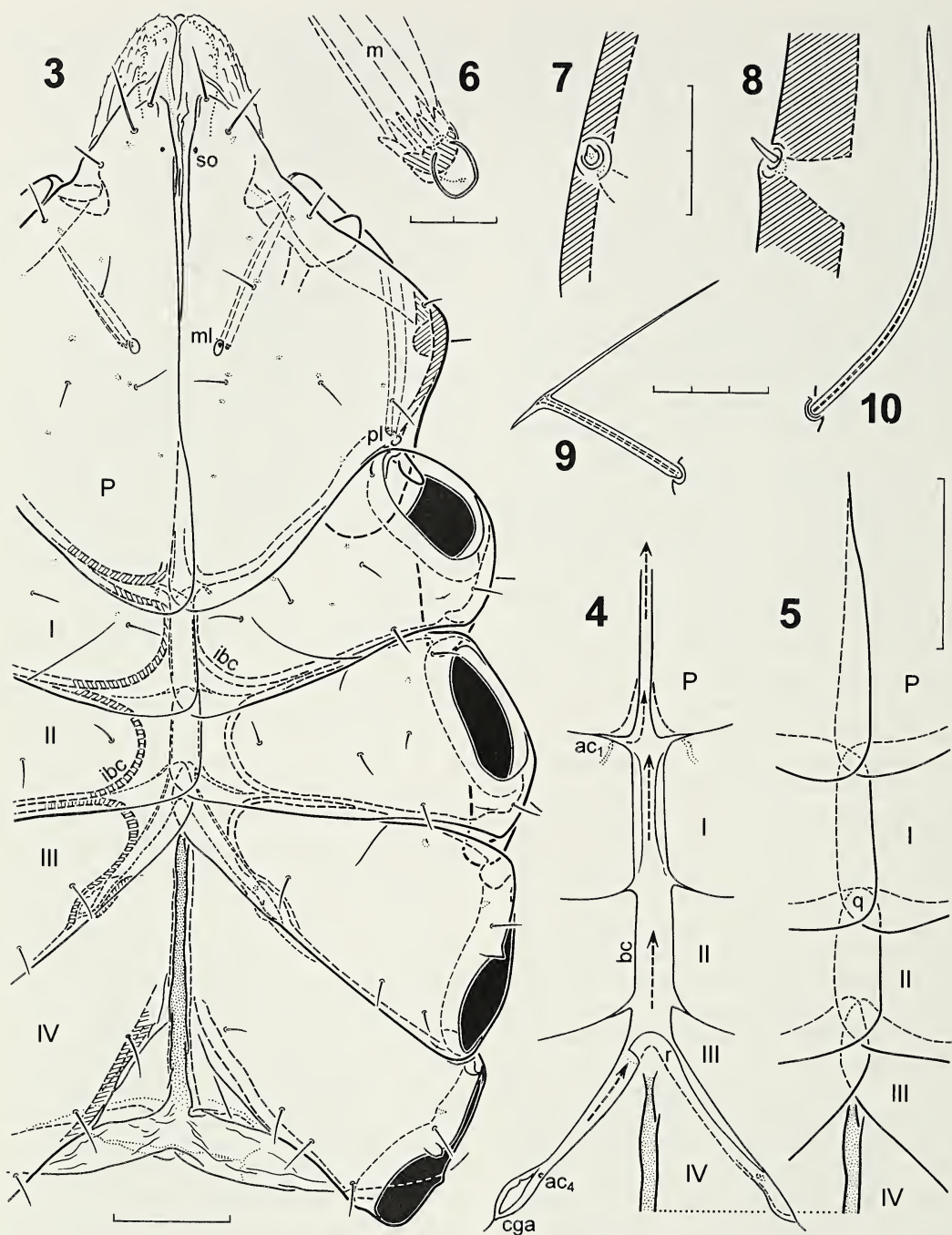
Figures 3–10.—Coxal region and cheliceral setae of Sternophoridae. 3–7, *Afrosternophorus* aff. *hirsti*, female (MH 611.08). 3, Coxae, ventral view; 4, Coxal canal (most of posterior rim removed from right coxa IV; arrows indicate inferred flow of secretions); 5, Overlapping of coxal tecta; 6, Right median maxillary lyrifissure, with apodeme (hatched) and muscle; 7, Left suboral seta. 8–10, *Garyops depressus*, female (WM 7186); 8, Left suboral seta; 9, Abnormal seta *es* of left chelicera; 10, Normal seta *es* of right chelicera. Abbreviations: *I–IV* = coxae I–IV; ac_1, ac_4 = ducts of accessory glands; *bc* = border of canal; *cga* = atrium of coxal gland; *ibc* = internal border of coxa; *m* = muscle; *ml* = median maxillary lyrifissure; *P* = coxa of palp; *pl* = posterior maxillary lyrifissure; *q* = point at which four tecta overlap; *r* = posterior rim of coxal canal; *so* = suboral seta. Scale divisions: 0.1 mm (Figs. 3–5); 0.01 mm (Figs. 6–10).

delimit the 'pseudosternum' and are the only parts that have moved antiaxially. The cuticle between them (the pseudosternum) is neither membranous nor desclerotized—it is simply thinner than that of the rest of the coxa. Closer to the midline lies the second series of apparent borders (*bc*), which represent the edge of a curve seen in tangent. These curves correspond to a furrow between the coxae or, more exactly, a canal. It is only once the nature of this canal is understood that the function of the tecta becomes clearer.

Coxal canal.—The coxal glands of most arachnids are associated with canals or ducts that carry their secretions towards the oral region. Pseudoscorpions are no exception, but the course followed the secretions of their glands has received little attention. This may be due to the obscurity of the opening on the posterior margin of coxa III, which is covered by the posterior margin of coxa IV. Heurtault (1973) even concluded that the coxal gland lacked an external opening and was solely endocrine, based on histological studies of *Neobisium caporiaccoi* Heurtault 1966.

Hammen (1986: fig. 4B; 1989: fig. 115B) illustrated a tiny 'orifice' associated with the intercoxal tubercle of *Chthonius tenuis* L. Koch 1873. He interpreted the intercoxal tubercle as a vestigial sternapophysis and noted that sternapophyses are often associated with the 'taenidia' (canals) of coxal glands. Unfortunately, the nature of this 'orifice' is unclear. It is certainly not the opening of the coxal gland (which is larger and situated further along coxa III) and I have not been able to find anything similar in *Chthonius*. Nevertheless, Hammen's implication that the secretions of the coxal glands flow between the coxae is correct. This becomes evident when other families are considered, many of which show a well defined canal, running from the openings of the coxal glands to the oral region.

The Sternophoridae are one of the most convenient groups in which to study the course of the coxal canal. This is because the flattening of the coxae reduces the three dimensional nature of the canal, simplifying the observations and their interpretation. Although this flattening also involves some unusual modifications, the basic form is similar to that found in other families and can therefore serve as an example.

Each coxal gland of Sternophoridae opens into a large cavity in the posterior margin of coxa III (Fig. 4: *cga*). This cavity, here termed the coxal gland atrium, also contains the openings of smaller gland ducts (one in *A.* aff. *hirsti,* two in *A. cylindrimanus*), which are assumed to belong to the anterior accessory glands (*ac₄*) (acinous glands of coxa IV; Heurtault 1973). The secretions of the accessory and coxal glands flow into the two branches of the canal between coxae III and IV (Fig. 4). The fluid continues along the unpaired median canal, which receives the secretions of another pair of accessory glands (presumably *ac₁*) at the anteromedian corners of coxa I. The presence of small branches of the canal between coxae I/II and II/III, suggests that secretions from the accessory glands of coxae II and III (not observed) may also flow into the canal. The combined secretions then flow into the oral cavity, which marks the end of the canal.

The course of the coxal canal is shown in Fig. 4. The drawing has been simplified by omitting the tecta, the bases of which correspond to the apparent lateral borders of the canal (*bc*) in ventral view. The posterior branches of the canal are bordered by an extended rim (or minitectum), which runs continuously along the anterior borders of coxae IV (Fig. 4: *r*). The fact that the rim crosses the midline without interruption is significant for two reasons. Firstly, it shows that the canal is closed posteriorly, removing any possibility of fluid flowing backwards along the space between coxae IV. Secondly, it shows that the anteromedian borders of coxae IV are fused. In fact, the canal is sclerotized for much of its length, which means that the other leg coxae are fused. This can be inferred from the porosity of the canal, which extends to the base of coxae I. Pore canals are typical of the sclerotized parts of pseudoscorpions and are never found on the membranes. This fusion is probably partial in the case of coxae I, which seem to have retained faint traces of their original borders. It appears that the floor of the canal was formed by a simultaneous sclerotization of the original intercoxal membrane and incorporation of the original coxal margins. The paraxial borders of coxae IV are free for most of their length, being separated by an ordinary intercoxal membrane (shown stippled in Fig. 4).

As yet, the presence of fluids in the canal

has only been directly observed in the cher-netid *Lamprochernes savignyi* (Simon 1881). Because the coxae are still relatively mobile in this species, the movement of fluid can be observed if a live specimen is trapped beneath a coverslip. As the animal struggles to free itself, the coxae move apart medially, reveal-ing the fluid in the coxal canal. The fluid is clear and inconspicuous in transmitted light, but its presence is evident from the meniscus that moves back and forth as the coxae open and close.

There can be little doubt that the secretions of the coxal glands follow the same course in all pseudoscorpions, even when there are no obvious modifications of the coxal margins (as Chthonioidea and most Neobisioidea). In-direct evidence for this is provided by the sim-ilarity of the positions of the glands and the presence of modifications facilitating the flow between coxae I and the palpcoxae. It is al-ready known that 'washing fluid' moves from and to the oral region along intercoxal space in the Chthonioidea and Neobisiidae (Wey-goldt 1966, 1969; Judson 1990). Indeed, the assumption that this fluid is produced by oral glands now seems questionable: it could equally be produced by the coxal glands.

Returning to the coxal tecta, it is evident that they serve to cover the canal, closing it off from the exterior. While it is possible that they form part of the canal (meaning that they are in contact with the secretions), their pri-mary function is probably one of protection. Because Sternophoridae live in confined spac-es, it is presumably important to prevent the fluid from coming into contact with the sub-strate or the canal from being blocked by de-bris. Similar tecta are also present in *Apo-cheiridium* Chamberlin 1924, another strongly flattened genus, adapted to living in tight bark-crevices. The covering of the canal var-ies in other groups, ranging from a simple rim to a membranous extension.

The coxal canal of pseudoscorpions pro-vides a remarkable parallel to the podoce-phalic canal of actinotrichid mites. Although they occupy different positions (the podoce-phalic canal runs laterally, above the anterior coxae), each receives the secretions of the coxal glands and accessory (non-nephridial) glands. The podocephalic canal also shows the same tendency to become covered by tecta

and may even become completely internal in some Prostigmata (Grandjean 1938).

Maxillary lyrifissures.—Chamberlin (1931) noted that the median and posterior maxillary lyrifissures of certain Cheliferoidea show spe-cialized internal processes, from which he in-ferred that they had evolved into a different sensory structure from the normal lyriform or-gans. Although not mentioned in his text, Chamberlin (1931: fig. 20F) also figured an internal process of the median manducatory lyrifissure in *Garyops sini*. Similar modifica-tions can also be found in Cheiridioidea, Gar-ypoidea and Neobisioidea, though their de-velopment is more variable and less well marked in the latter group.

These internal structures are in fact apode-mes. The median manducatory lyrifissure is attached to one of the flexor muscles of the trochanter and the lateral lyrifissure is attached to an extensor muscle (Figs. 3, 6). The apo-deme itself is a continuation of the plate of cuticle bounded by the lyrifissure and is at-tached to the muscles via short tendons. As the muscles contract, the plate will be pulled inwards. Chamberlin's interpretation is prob-ably correct, in the sense that the lyrifissure must be detecting contractions of the attached muscle, rather than stresses across the cuticle.

It should be noted that an analogous curv-ing has occurred in the dorsal femoral lyrifis-sure of Chernetidae, Cheliferidae and Atem-nidae (Harvey 1992). However, there is no indication of an apodeme associated with these lyrifissures.

Suboral seta.—Judson (1985) briefly dis-cussed the presence of a modified 'sensory seta' at the mesal border of the manducatory process in pseudoscorpions. Because the term 'sensory seta' is almost meaningless, it is here replaced by *suboral seta*.

The suboral setae of Sternophoridae are particularly interesting because they show the most reduced form yet known. The suboral setae of *Garyops depressus* are small, but oth-erwise unremarkable (Fig. 8). In contrast, those of *Idiogaryops paludis* and the *Afro-sternophorus* species examined have the hair shortened to the point where its height scarce-ly exceeds its breadth (e.g., Fig. 7). At low magnifications, it appears as a mere dot in the middle of its areole (Fig. 6) and could easily be mistaken for the base of a broken hair.

However, the seta has retained its lumen and tapers to a point.

These reductions confirm that there is an evolutionary trend towards a decrease in the size of the suboral seta. In view of the extreme reduction seen in sternophorids, it is possible that this regression can lead to the complete loss of the suboral seta. This might explain the curious absence of suboral setae in the Pseudogarypidae, whose sister group—the Feaellidae—have short suboral setae.

Cheliceral setae.—There is an interesting parallel between the form of the vestitural setae and certain setae on the cheliceral hand in pseudoscorpions. When the dorsal vestitural setae are modified in a particular way, the proximal setae of the chelicerae tend to have the same morphology, although it may be less marked. This parallel differentiation is most clearly seen in the Panctenodactyli, partly because they often have strongly modified vestitural setae and partly because of the small number of fundamental setae (five or less). Excluding cases of secondary multiplication (neotrichy), it is setae b and sb that follow the form of the vestitural setae, whereas setae is and ls remain simple and acuminate. Seta es is sometimes modified like b and sb, but is more often simple, perhaps due to its lower position (ventral vestitural setae also tend to be simple).

Harvey (1985) noted that seta b (=bs) of Sternophoridae differs from the other cheliceral setae in being blunt. This unusual form is found in the dorsal vestitural setae of all Sternophoridae. Assuming that the rule of parallel differentiation holds in this family, it provides a simple way of deciding which of the original five setae has been lost from the cheliceral hand. According to Chamberlin (1931) and Harvey (1985), it is ls that has been lost, whereas Hoff (1963) interpreted the missing seta as sb. Excluding es (the identity of which is not in question), if ls were missing, one would expect two of the remaining setae (b and sb) to be blunt. The fact that only one blunt seta (b) is present indicates that the missing seta is sb, thus confirming Hoff's view.

The female of *G. depressus* examined here shows an unusual abnormality of seta es on the left chelicera. The seta is roughly T-shaped, except that one of the arms is much longer than the other (Fig. 9). The lumen of the seta is enlarged at the node, but does not extend much further (*cf.* Figs. 9 and 10), which means that the hair is thinner than usual beyond this point. The fact that the bifurcation occurred so far from the base suggests that the anomaly was caused by mechanical deformation during ecdysis, rather than by a doubling of the hair.

Trichobothriotaxy.—Harvey (1985) showed that previous reports of sternophorids with a full complement of eight trichobothria on the fixed finger of the chela were due to errors of observation. Schawaller (1991) later illustrated a female of *Afrosternophorus cylindrimanus* (Beier) [possibly *A. dawydoffi* (Beier 1951), according to Schawaller (1994)] as having four trichobothria in the internal series of the fixed finger. However, the extra, distal trichobothrium in the internal series was drawn by mistake (W. Schawaller *in litt.*). The loss of trichobothrium *isb* therefore remains a synapomorphy of the Sternophoridae.

ACKNOWLEDGEMENTS

LITERATURE CITED

Banks, N. 1909. New Pseudoscorpionida. Canadian Entomol., 41:303–307.

Baroni Urbani, C. 1980. The first fossil species of the Australian ant genus *Leptomyrmex* in amber from the Dominican Republic (amber collection Stuttgart: Hymenoptera, Formicidae. III: Leptomyrmicini). Stuttgarter Beitr. Naturk., (B) 62:1–10.

Chamberlin, J.C. 1923. New and little known pseudoscorpions, principally from the islands and ad-

jacent shores of the Gulf of California. Proc. California Acad. Sci., (4) 12:353–387.

Chamberlin, J.C. 1931. The arachnid order Chelonethida. Stanford Univ. Publ., Univ. Ser., (Biol. Sci.) 7:1–284.

Chamberlin, J.C. 1932. On some false scorpions of the superfamily Cheiridioidea (Arachnida – Chelonethida). Pan-Pacific Entomol., 8:137–144.

Grandjean, F. 1938. Observations sur les Bdelles (Acariens). Ann. Soc. Entomol. France, 107:1–24.

Grimaldi, D.A., E. Bonwich, M. Delannoy & S. Doberstein. 1994. Electron microscopic studies of mummified tissues in amber fossils. American Mus. Novit., 3097:1–31.

Hammen, L. van der. 1986. Comparative studies in Chelicerata IV. Apatellata, Arachnida, Scorpionida, Xiphosura. Zool. Verhand., 226:1–52.

Hammen, L. van der. 1989. An Introduction to Comparative Arachnology. SPB Academic Publishing bv, The Hague.

Harvey, M.S. 1985. The systematics of the family Sternophoridae (Pseudoscorpionida). J. Arachnol., 13:141–209.

Harvey, M.S. 1992. The phylogeny and classification of the Pseudoscorpionida (Chelicerata: Arachnida). Invert. Taxon., 6:1373–1435.

Heurtault, J. 1973. Contribution à la connaissance biologique et anatomo-physiologique des Pseudoscorpions. Bull. Mus. Natl. Hist. Nat., Paris, (3) 124 (Zool. 96):561–670.

Hoff, C.C. 1963. Sternophorid pseudoscorpions, chiefly from Florida. American Mus. Novit., 1875:1–36.

Hounsome, M.V. 1980. The terrestrial fauna (excluding birds and insects) of Little Cayman. *In* Geography and Ecology of Little Cayman (D.R. Stoddart & M.E.C. Giglioli, eds). Atoll Res. Bull., 241:81–90.

Iturralde-Vinent, M.A. & R.D.E. MacPhee. 1996. Age and paleogeographical origin of Dominican amber. Science, 273:1850–1852.

Judson, M.L.I. 1985. Redescription of *Myrmochernes* Tullgren (Chelonethida: Chernetidae). Bull. British Arachnol. Soc., 6:321–327.

Judson, M.L.I. 1990. Observations on the form and function of the coxal spines of some chthonioid

pseudoscorpions from Cameroon (Arachnida, Chelonethida). Acta Zool. Fennica, 190:195–198.

Mahnert, V. 1985. Weitere Pseudoskorpione (Arachnida) aus dem zentralen Amazonasgebiet (Brasilien). Amazoniana, 9:215–241.

Schawaller, W. 1980a. Erstnachweis tertiärer Pseudoskorpione (Chernetidae) in Dominikanischem Bernstein (Stuttgarter Bernsteinsammlung: Arachnida, Pseudoscorpionidea). Stuttgarter Beitr. Naturk., (B) 57:1–20.

Schawaller, W. 1980b. Fossile Chthoniidae in Dominikanischem Bernstein, mit phylogenetischen Anmerkungen (Stuttgarter Bernsteinsammlung: Arachnida, Pseudoscorpionidea). Stuttgarter Beitr. Naturk., (B) 63:1–19.

Schawaller, W. 1981a. Pseudoskorpione (Cheliferidae) phoretisch auf Käfern (Platypodidae) in Dominikanischem Bernstein (Stuttgarter Bernsteinsammlung: Arachnida, Pseudoscorpionidea und Coleoptera). Stuttgarter Beitr. Naturk., (B) 71:1–17.

Schawaller, W. 1981b. Cheiridiidae in Dominikanischem Bernstein, mit Anmerkungen zur morphologischen Variabilität (Stuttgarter Bernsteinsammlung: Arachnida, Pseudoscorpionidea). Stuttgarter Beitr. Naturk., (B) 75:1–14.

Schawaller, W. 1991. Neue Pseudoskorpion-Funde aus dem Nepal-Himalaya, III (Arachnida: Pseudoscorpiones). Rev. Suisse Zool., 98:769–789.

Schawaller, W. 1994. Pseudoskorpione aus Thailand (Arachnida: Pseudoscorpiones). Rev. Suisse Zool., 101:725–759.

Schawaller, W., W.A. Shear & P.M. Bonamo. 1991. The first Paleozoic pseudoscorpions (Arachnida, Pseudoscorpionida). American Mus. Novit., 3009:1–17.

Weygoldt, P. 1966. Vergleichende Untersuchungen zur Fortpflanzungsbiologie der Pseudoscorpione. Beobachtungen über das Verhalten, die Samenübertragungsweisen und die Spermatophoren einiger einheimischer Arten. Z. Morphol. Ökol. Tiere, 56:39–92.

Weygoldt, P. 1969. The biology of pseudoscorpions. Harvard Univ. Press, Cambridge.

PSEUDOSCORPION GROUPS WITH BIPOLAR DISTRIBUTIONS: A NEW GENUS FROM TASMANIA RELATED TO THE HOLARCTIC *SYARINUS* (ARACHNIDA, PSEUDOSCORPIONES[1], SYARINIDAE)

Mark S. Harvey: Department of Terrestrial Invertebrates, Western Australian Museum, Francis Street, Perth, Western Australia 6000, Australia

ABSTRACT.   A new genus *Anysrius* is proposed for two new species from Tasmania, Australia: *A. chamberlini* (type species) and *A. brochus. Anysrius* represents the sister-genus to the northern hemisphere genus *Syarinus* Chamberlin, but males differ in differences in the morphology of sternite II and IV. The biogeographic aspects of the new discovery are examined, and the *Syarinus-Anysrius* clade is considered to represent an ancient relict which evolved prior to the breakup of Pangea during the Mesozoic. This distribution pattern is considered to be 'bipolar' and is compared with that of the pseudoscorpion family Pseudogarypidae, which is also known from Tasmania and the Holarctic.

Recognizable bipolar or amphi-arctic distributions (i.e., where extant taxa occur in northern and southern latitudes but are absent from tropical zones) seem to be uncommon amongst arachnids, with probably one of the most clear-cut examples being the pseudoscorpion family Pseudogarypidae. This family is represented by a sole Tasmanian genus and species, *Neopseudogarypus scutellatus* Morris 1948, six North American species of *Pseudogarypus* Ellingsen 1909, and three Tertiary species of *Pseudogarypus* described from European Baltic Amber (see Harvey 1991a).

Similar distribution patterns were reported for the pseudoscorpion family Syarinidae by Harvey (1996), who briefly discussed the occurrence of a new genus from Tasmania which appeared to be most similar to *Syarinus* Chamberlin 1925 from North America and Europe. I here take the opportunity to examine in more detail the taxonomic and biogeographic anomalies posed by the Tasmanian species, and also examine the presence of sternal modifications in male syarinids.

The material examined during this study is lodged in the following repositories: American Museum of Natural History, New York (AMNH); Australian National Insect Collection, Canberra (ANIC); Florida State Collection of

Arthropods, Gainesville (FSCA); Museum of Victoria, Melbourne (NMV); Tasmanian Museum and Art Gallery, Hobart (TMAG); and Western Australian Museum, Perth (WAM). Terminology follows Chamberlin (1931) and Harvey (1992), with measurements being taken to the nearest 0.005 mm.

TAXONOMY

Syarinidae Chamberlin

Syarinidae Chamberlin 1930: 38; Harvey 1991a: 417 (full synonymy).

Remarks.—The Syarinidae were characterized by Muchmore (1982a, 1982b) and Harvey (1992), but there are several morphological anomalies in some genera which suggest that the family may not be monophyletic. Muchmore (1982b) highlighted the presence of a shortened and lanceolate trichobothrium *t,* a character state found in *Syarinus, Ideobisium* Balzan 1892, *Ideoblothrus* Balzan 1892, *Nannobisium* Beier 1931, *Chitrella* Beier 1932 and *Microblothrus* Mahnert 1985 (Muchmore 1982b; Mahnert 1985; Harvey, pers. obs.), and the new genus described below. However, *t* is acuminate and not particularly shortened in the remaining syarinid genera *Microcreagrina* Beier 1961, *Microcreagrella* Beier 1961, *Hadoblothrus* Beier 1952, *Pseudoblothrus* Beier 1931 and *Troglobisium* Beier 1939 (Muchmore 1982b). The nature of *t* in *Aglaochitra* Chamberlin 1952 is

---

unknown, as is that of *Chitrellina* Muchmore 1996 due to the loss of both trichobothria in the sole specimen (see Muchmore 1996).

The Australian syarinid fauna consists of two described species of *Ideoblothrus,* numerous undescribed species of *Ideoblothrus* and *Ideobisium* (Harvey 1991b; unpubl. data), and two undescribed species of a new genus from Tasmania, which is clearly unrelated to either *Ideoblothrus* or *Ideobisium.*

The two genera discussed below share a number of significant apomorphic features, which clearly place them as sister-groups. These include: (1) trichobothrium *isb* situated on internal margin of fixed chelal finger; (2) pedipalpal coxa rounded and with 2 setae; (3) junction between femur and patella IV strongly oblique; (4) male sternite IV with one or median cribrate areas.

In order to interpret the similarities and differences between the Tasmanian and Holarctic species, I here fully describe the Tasmanian species and make observations upon some species of *Syarinus.*

Anysrius new genus

Type species.—*Anysrius chamberlini* new species.

Etymology.—The generic epithet is an anagram of *Syarinus,* and is masculine in gender.

Diagnosis.—Distinguished from all Syarinidae, except *Syarinus,* by the presence of trichobothrium *isb* situated on internal face of fixed chelal finger (Figs. 1, 6, 19, 22), apex of pedipalpal coxa rounded and with 2 setae, the strongly oblique junction between femur and patella IV (Figs. 9, 28); subterminal tarsal seta acuminate (Figs. 8, 9, 28); and male sternite IV with median cribrate area (Figs. 16, 29), but apparently without associated glands. *Anysrius* differs from *Syarinus* by male sternite II bearing an external lobe and median cribrate area (Figs. 16, 29), and the single median cribrate area of male sternite IV (Figs. 16, 29).

Description.—*Pedipalps:* Apex of coxa rounded and with 2 setae; chelal fingers somewhat curved; chelal teeth contiguous (Figs. 1–4, 19–21); venom apparatus absent from movable finger; venom duct of fixed finger short (Figs. 1–4, 19–21). Fixed chelal finger with 8 trichobothria, movable chelal finger with 4 trichobothria (Figs. 1, 22); trichobothria *est, et* and *it* situated in distal portion of fixed finger,

eb, esb, ib, isb and *ist* situated in basal portion of fixed finger; *isb* situated on internal face of fixed chelal finger; *sb, st* and *t* closely spaced near middle of movable finger; *t* lanceolate (Fig. 5). Chelicera (Figs. 11, 24, 25): hand with 5 setae, movable finger with 1 sub-distal seta; lamina exterior and velum absent; flagellum composed of 6 blades, the 4 distal blades with several anteriorly-directed spinules (Figs. 14, 27); galea of ♂ small and usually acuminate (Figs. 12, 24), of ♀ trifurcate with each ramus terminally trifurcate or bifurcate (Figs. 13, 25). Carapace (Figs. 10, 23): subquadrate, with 1 pair of eyes, anterior eyes small and flat, posterior eyes absent. Pleural membrane generally longitudinally striate, although near cephalic region it becomes slightly granulate. ♂ sternite II with median cribrate area and external lobe (Figs. 16, 29); ♂ sternite IV with single median cribrate area (Figs. 16, 29), but apparently without associated glands. Male genital atrium without internal setae. Female genitalia (Figs. 18, 31) with 1 median and 2 small lateral cribriform plates, with very few pores; spermathecae absent. Spiracles simple, with spiracular helix; anterior pair of tracheae long, ramifying into tracheoles when above coxae IV; posterior pair of tracheae short, ramifying into tracheoles almost immediately; spiracular plates with setae. *Legs:* (Figs. 8, 9, 28) Junction between femur and patella I nearly perpendicular; femora I and II without basi-dorsal mound; junction between femur and patella IV strongly oblique; metatarsus and tarsus of all legs separate; subterminal tarsal seta acuminate; arolium slightly shorter than claws.

Included species.—*Anysrius chamberlini* new species and *A. brochus* new species.

Distribution.—Apparently endemic to Tasmania.

Remarks.—Although the two species referred to *Anysrius* below are clearly sister-groups, there may be grounds for the placement of each species in a separate genus. This is solely based upon autapomorphies present in males of each species. In *A. chamberlini,* the male pedipalpal patella bears numerous small specialized blunt setae which are lacking in *Syarinus* and *A. brochus,* and in *A. brochus* the male movable cheliceral finger bears several dorsal protuberances which are lacking in *Syarinus* and *A. chamberlini.* However, the two species share two apomorphies lack-

ing in all other syarinids, including *Syarinus*: male sternite II with an external lobe and a median cribrate area. For this reason, it seems prudent to retain them in a single genus until further species are discovered and until a detailed review of the morphology of members of the genus *Syarinus* can be undertaken (see below).

The external lobe found on male sternite II of *Anysrius* spp. is apparently unique within the Pseudoscorpiones, and its function is completely unknown. It is very weakly sclerotized and although it bears a number of small external pores (Figs. 16, 29), no internal glandular system could be detected which may connect to the lobe.

Anysrius chamberlini new species
(Figs. 1–18)

Undescribed genus and species.—Harvey 1990: 158–159, fig. 4; Harvey 1996: 258.

Types.—Male holotype from Frodshams Pass, Tasmania, Australia [42°49′S, 146°23′E], thamnic rainforest litter, 18 November 1988 (P. Greenslade) (ANIC, spirit). Paratypes, all from **Australia**: *Tasmania*: 2♀, 1 tritonymph, same data as holotype (ANIC, spirit); 1♂1♀, 2 km S. of Frodshams Pass, 42°50′S, 146°23′E, rainforest litter berlesate, 24 January 1983 (I.D. Naumann, J.C. Cardale) (ANIC, slides); 1 deutonymph, Frodshams Pass, in rainforest leaf litter, 23 March 1985 (P. Greenslade) (ANIC, spirit); 1 protonymph, Frodshams Pass, 42°49′S, 146°23′E, rainforest leaf litter and log debris, 22 November 1986 (M.S. Harvey, P.K. Lillywhite) (WAM, spirit); 81♀, 2 tritonymphs, 2 deutonymphs, divide between Huon and Florentine Rivers, Scotts Peak Road, 42°48′S, 146°22′E, ex moss, myrtle forest, 3 May 1973 (J.L. Hickman) (TMAG, spirit); 1♀, 1 tritonymph, 1 deutonymph, same data (WAM, spirit).

Etymology.—The specific epithet is in honor of Joseph Conrad Chamberlin.

Diagnosis.—Males of *A. chamberlini* differs from those of *A. brochus* by the lack of external teeth on the movable cheliceral finger (Fig. 11), and the presence of *ca.* 25 dorsal specialized blunt setae on the dorsal surface of the pedipalpal patella (Figs. 6, 7). Females differ by the poorly granulate pedipalpal femur and chelal hand.

Description.—*Adults:* Pedipalps and cara-

pace red-brown, legs slightly paler, remainder of body pale. Pedipalps (Fig. 6): apex of coxa rounded and with 2 setae; trochanter 1.96 (♂), 1.89 (♀), femur 2.83 (♂), 2.69 (♀), patella 2.00 (♂), 1.95 (♀), chela (with pedicel) 2.93 (♂), 2.90 (♀), chela (without pedicel) 2.73 (♂, ♀), hand (without pedicel) 1.13 (♂), 1.33 (♀) times longer than broad, movable finger 1.45 (♂), 1.06 (♀) times longer than hand (without pedicel). Anterior face of femur and internal face of chela very slightly granulate; patella with *ca.* 25 dorsal specialized blunt setae (Fig. 7). Fixed chelal finger with 8 trichobothria, movable chelal finger with 4 trichobothria (Fig. 1); *est, et* and *it* situated in distal portion of fixed finger; *eb, esb, ib, isb* and *ist* situated in basal portion of fixed finger; *isb* situated on internal face of fixed chelal finger; *sb, st* and *t* closely spaced near middle of movable finger; *t* lanceolate (Fig. 5). Chelal teeth contiguous (Fig. 1), fixed finger with 34 (♂), 30 (♀), and movable finger with 39 (♂), 35 (♀) teeth. Chelicera (Fig. 11): hand with 5 setae, movable finger with 1 sub-distal seta; fixed finger with 14 (♂), 13 (♀) teeth on inner surface; movable finger with 11 (♂, ♀) teeth on inner surface; serrula exterior with 19 (♂, ♀) lamellae; flagellum of 6 blades, the 4 distal blades with several anteriorly-directed spinules (Fig. 14); galea of ♂ small and usually acuminate, but trifurcate on left chelicera of holotype (Fig. 12), of ♀ trifurcate with each ramus terminally trifurcate or bifurcate (Fig. 15). Carapace (Fig. 10) with a total of 32 (♂), 28 (♀) setae, including 4 setae on anterior margin and 8 setae on posterior margin, 1.01 (♂), 0.91 (♀) times longer than broad; 2 small eyes, posterior pair absent. Pleural membrane generally longitudinally striate, although near the cephalic region it becomes slightly granulate. Tergal chaetotaxy: ♂, 10: 11: 12: 15: 14: 14: 17: 15: 13: 13: 5: 2; ♀, 10: 10: 13: 14: 15: 15: 15: 15: 14: 12: 4: 2. Sternal chaetotaxy: ♂, 12: (2)15[0](2): (2)15(2): 12: 16: 16: 16: 15: 12: 7: 2; ♀, 8: (1)14(2): (2)11(2): 13: 15: 14: 14: 14: 12: 6: 2. Genital opercula of ♀ not unusual; those of ♂ with median cribrate area on sternite II and on sternite IV (Fig. 16), sternite II with external lobe (Fig. 16). Male genitalia (Fig. 17) lateral apodeme and lateral rod fused along entire length; ejaculatory canal atrium large; median genital sac undivided; genital atrium without internal setae. Female genitalia (Fig. 18) with 1 me-
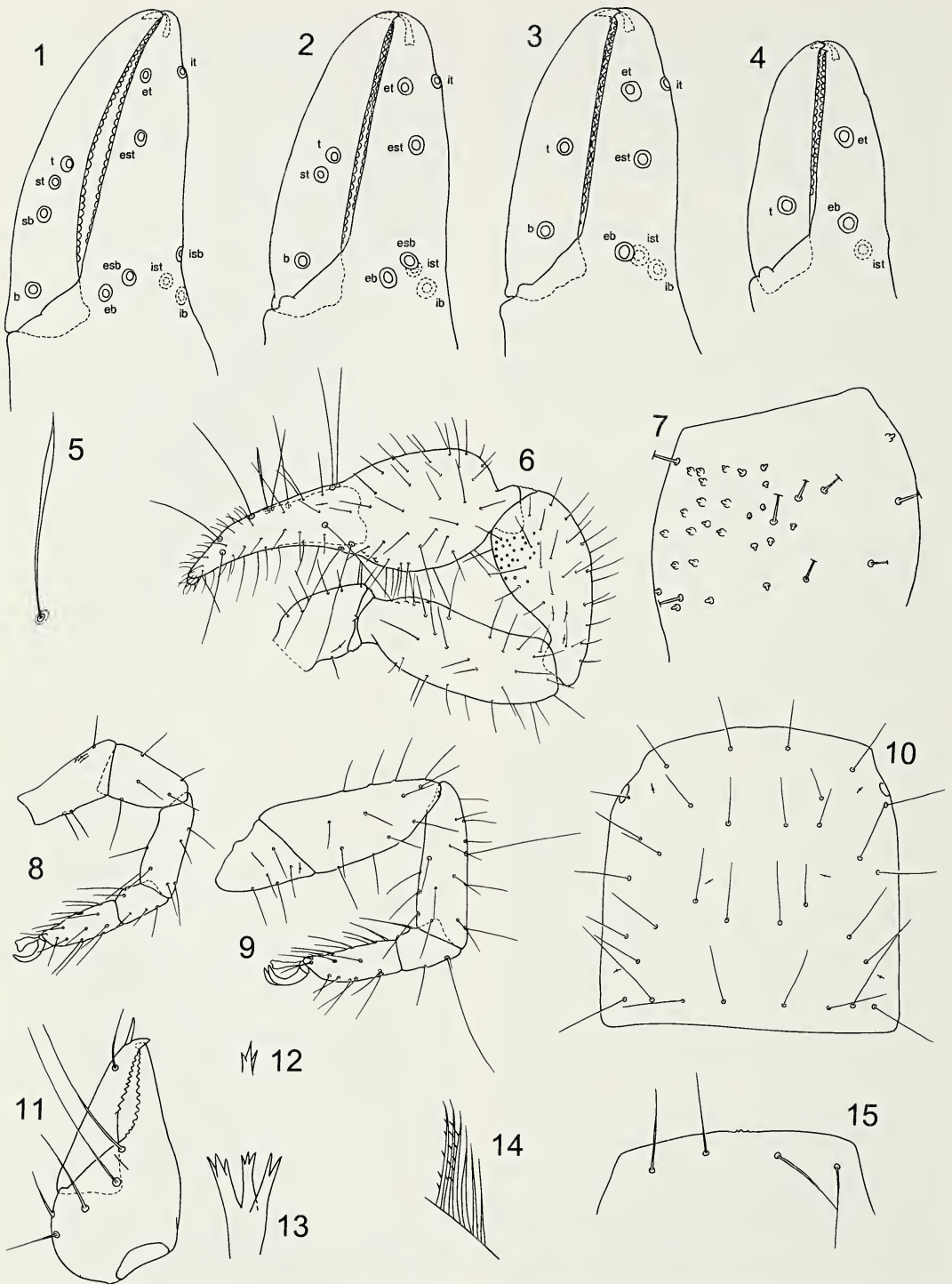
Figures 1–15.—*Anysrius chamberlini* new species, male holotype unless stated otherwise. 1–4, Left chelae, lateral: 1, Male; 2, Tritonymph paratype; 3, Deutonymph paratype; 4, Protonymph paratype; 5, Trichobothrium *t*; 6, Right pedipalp, dorsal; 7, Right pedipalpal patella, showing detail of specialized blunt setae; 8, Left leg I; 9, Left leg IV; 10, Carapace; 11, Left chelicera, dorsal; 12, Galea; 13, Galea, female paratype; 14, Flagellum; 15, Carapace, anterior margin, protonymph.
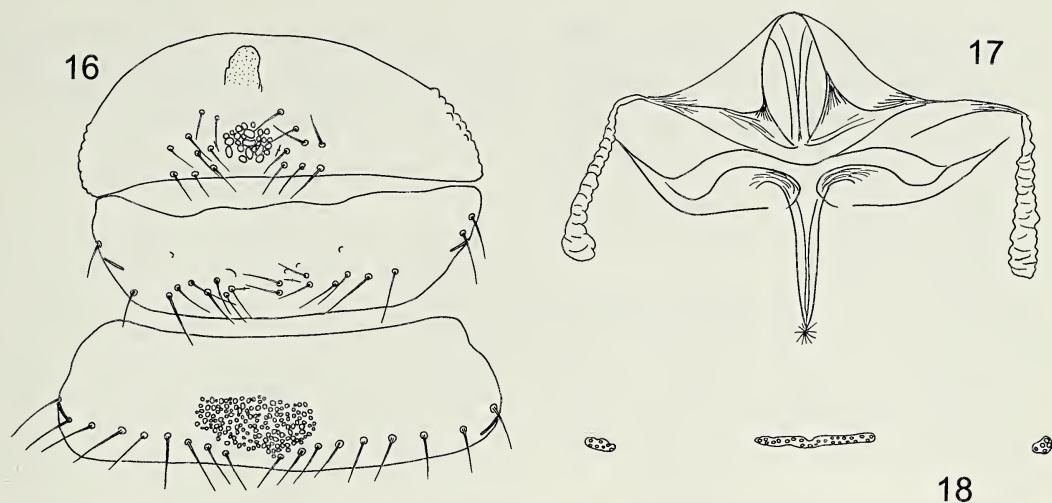
Figures 16–18.—*Anysrius chamberlini* new species. 16–17, Male paratype: 16, Genital sternites, ventral; 17, Genitalia, ventral; 18, Genitalia, ventral, female paratype.

dian and 2 small lateral cribriform plates, with very few pores; spermathecae absent. Legs (Figs. 8, 9): moderately stout; leg I with femur 1.25 (♂), 1.32 (♀) times longer than patella; junction between femur and patella I nearly perpendicular; femur + patella IV 3.21 (♂), 3.20 (♀) times longer than deep; junction between femur and patella IV strongly oblique; tibia IV 3.40 (♂), 3.67 (♀) times longer than deep; tibia and metatarsus IV each with single sub-proximal tactile seta; subterminal tarsal seta acuminate; arolium not divided distally, slightly shorter than claws.

Dimensions (mm): Holotype ♂ (paratype ♀): Body length 1.570 (1.920). Pedipalps: trochanter 0.250/0.125 (0.255/0.135), femur 0.410/0.145 (0.430/0.160), patella 0.360/0.180 (0.360/0.185), chela (with pedicel) 0.660/0.225 (0.740/0.255), chela (without pedicel) 0.615 (0.695), hand length (without pedicel) 0.255 (0.340), movable finger length 0.370 (0.360). Chelicera 0.240/0.130 (0.270/0.155), movable finger length 0.175 (0.200). Carapace 0.410/0.405 (0.455/0.500); diameter of eye 0.030 (0.025). Leg I: femur 0.175/0.075 (0.185/0.080), patella 0.140/0.080 (0.140/0.085), tibia 0.160/0.060 (0.175/0.060), metatarsus 0.080/0.050 (0.085/0.050), tarsus 0.130/0.045 (0.130/0.045). Leg IV: femur + patella 0.370/0.115 (0.400/0.125), tibia 0.255/0.075 (0.275/0.075), metatarsus 0.095/0.60 (0.100/0.065), tarsus 0.145/0.055 (0.160/0.055).

Tritonymph: Pedipalps: trochanter 1.78, femur 2.58, patella 1.90, chela (with pedicel) 3.00, chela (without pedicel) 2.79 times longer than broad. Fixed finger with 7 trichobothria, movable finger with 3 trichobothria (Fig. 2); *eb, esb, est, et, ib, ist, it, b, sb* and *t* present, *t* lanceolate and shorter than other trichobothria. Chelicera: galea trifurcate, 2 rami terminally trifurcate, other bifurcate; hand with 5 setae, movable finger with 1 seta; fixed finger with 11 teeth, movable finger with 12 teeth; flagellum composed of 6 blades, the 3 distal blades with several anteriorly-directed spinules. Carapace 0.93 times longer than broad; epistome absent; one pair of small eyes present; with 26 setae including 4 setae on anterior margin and 8 setae on posterior margin. Legs as in adult.

Dimensions (mm): Body length 1.630. Pedipalps: trochanter 0.205/0.115, femur 0.335/0.130, patella 0.285/0.150, chela (with pedicel) 0.585/0.195, chela (without pedicel) 0.545, hand length (without pedicel) 0.280, movable finger length 0.270. Carapace 0.385/0.415.

Deutonymph: Pedipalps: trochanter 1.74, femur 2.50, patella 1.78, chela (with pedicel) 3.03, chela (without pedicel) 2.86 times longer than broad. Fixed finger with 6 trichobothria, movable finger with 2 trichobothria (Fig. 3); *eb, est, et, ib, ist, it, b* and *t* present, *t* lanceolate and slightly shorter than other trichobothria. Chelicera: galea trifurcate, 2 rami terminally divided, 1 ramus bifurcate and 1

trifurcate; hand with 5 setae, movable finger with 1 setae; fixed finger with 9 teeth, movable finger with 6 teeth; flagellum composed of 6 blades, the 4 distal blades with several anteriorly-directed spinules. Carapace 1.13 times longer than broad; epistome absent; eyes absent; with 20 setae, including 4 setae on anterior margin and 4 setae on posterior margin. Legs as in adult.

Dimensions (mm): Body length 0.700. Pedipalps: trochanter 0.165/0.095, femur 0.250/0.100, patella 0.205/0.115, chela (with pedicel) 0.440/0.145, chela (without pedicel) 0.415, hand length (without pedicel) 0.190, movable finger length 0.220. Carapace 0.300/0.265.

Protonymph: Pedipalps: trochanter 1.63, femur 2.06, patella 1.72, chela (with pedicel) 3.15, chela (without pedicel) 3.00 times longer than broad. Fixed finger with 3 trichobothria, movable finger with 1 trichobothrium (Fig. 4); *eb, et, ist* and *t* present, *t* not lanceolate. Chelicera: galea trifurcate, one ramus terminally divided, others simple; hand with 4 setae, movable finger without setae; fixed finger with 7 teeth, movable finger with 7 teeth; flagellum composed of 5 blades, the 3 distal blades with several anteriorly-directed spinules. Carapace 0.93 times longer than broad; an extremely small epistome present, consisting of 3 small, pointed processes (Fig. 15); eyes absent; with 20 setae including 4 setae on anterior margin and 4 setae on posterior margin. Legs as in adult.

Dimensions (mm): Body length 0.620. Pedipalps: trochanter 0.130/0.080, femur 0.175/0.085, patella 0.155/0.090, chela (with pedicel) 0.360/0.115, chela (without pedicel) 0.345, hand length (without pedicel) 0.165, movable finger length 0.195. Carapace 0.250/0.270.

Remarks.—The specialized blunt setae found on the male pedipalpal patella are apparently unique amongst the Pseudoscorpiones, and their morphology suggests they are modified setae rather than cuticular granules. They appear to sit in a small pit, which differs somewhat from the setae found on the pedipalp, since the rim is not as sharply defined. The cuticle from which they arise is otherwise not modified and canals cannot be detected in them. They are completely absent in all nymphs.

Anysrius chamberlini is known only from

two, adjacent localities in south-western Tasmania. The vegetation of both areas consists of remnant temperate rainforest, dominated by trees of the austral genus *Nothofagus.*

Anysrius brochus new species
(Figs. 19–31)

Types.—Male holotype, 1 ♀ paratype and 1 deutonymph paratype from 'Chatlee Road' site, Salmon River Forestry area, 41°04'S, 144°52'E, ex litter, '47 year old *Eucalyptus obliqua'*, wet sclerophyll, 19 March 1975 (J.L Hickman et al.) (TMAG J1861, slides). Paratypes, all from **Australia:** *Tasmania:* 1 ♀, 1 tritonymph, 'Chatlee Road 1' site, Salmon River Forestry area, 41°04'S, 144°52'E, ground litter, '1926-planted *Eucalyptus obliqua*', 27 August 1974 (J. Madden, L. Hill, A. Skuja) (TMAG J1687, spirit); 1 ♀, 1 tritonymph, 'Chatlee Road 4' site, Salmon River Forestry area, 41°04'S, 144°52'E, ground litter, '1926-planted *Eucalyptus obliqua*', 27 August 1974 (J. Madden, L. Hill, A. Skuja) (TMAG J1726, spirit); 1 ♂, 1 deutonymph, 'Chatlee Road 8' site, Salmon River Forestry area, 41°04'S, 144°52'E, ground litter, '1928-planted *Eucalyptus obliqua*', 29 November 1974 (J.L Hickman, J.L. Madden et al.) (TMAG J1691, spirit); 1 tritonymph, 2 deutonymphs, 'Chatlee Road' site, Salmon River Forestry area, 41°04'S, 144°52'E, ex soil, '46 year old *Eucalyptus obliqua*' forest, 19 March 1975 (J.L. Hickman et al.) (TMAG J1793, spirit); 1 ♀, 2 tritonymphs, 2 deutonymphs, 'Chatlee Road' area, Salmon River Forestry area, 41°04'S, 144°52'E, ground litter, '1928 *Eucalyptus obliqua*', 29 November 1974 (J. Madden, J.L. Hickman et al.) (TMAG J1692, spirit).

Etymology.—The specific epithet refers to the cheliceral teeth of the male (*brochus* Latin, projection of teeth).

Diagnosis.—Distinguished from *A. chamberlini* by the possession of external teeth on the movable cheliceral finger of the male (Figs. 24, 26), and by the absence of specialized blunt setae on the male pedipalpal patella (Fig. 22). Females differ from those of *A. chamberlini* by the strongly granulate pedipalpal femur and chelal hand.

Description.—*Adult:* Pedipalps and carapace red-brown, legs slightly paler, remainder of body pale. Pedipalps (Fig. 22): apex of coxa rounded and with 2 setae; trochanter
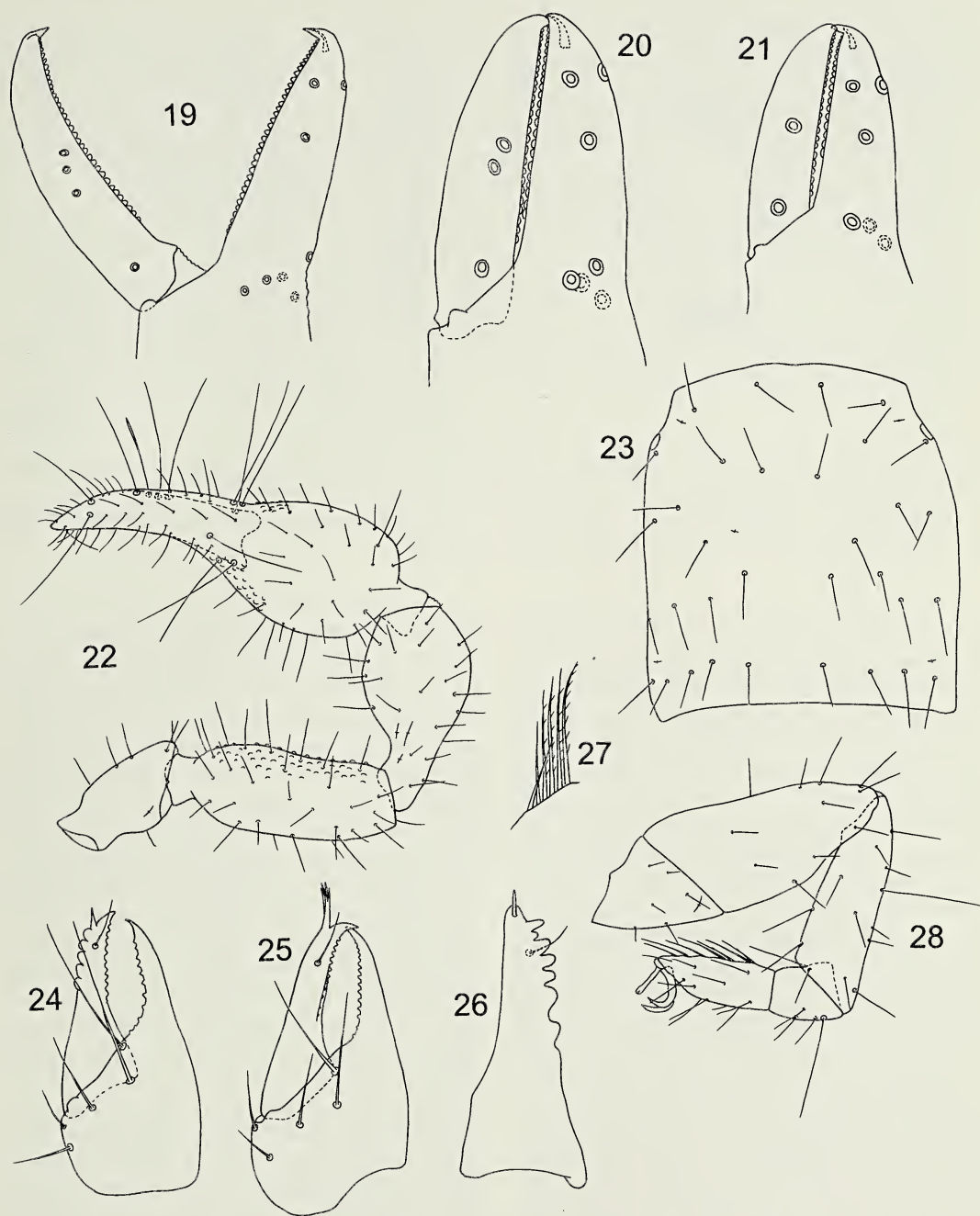
Figures 19–28.—*Anysrius brochus* new species, male holotype unless stated otherwise. 19–21, Left chelae, lateral: 19, Male; 20, Tritonymph paratype; 21, Deutonymph paratype; 22, Right pedipalp, dorsal; 23, Carapace; 24, Left chelicera, dorsal, male paratype; 25, Left chelicera, dorsal, female paratype; 26, Left movable cheliceral finger, lateral; 27, Flagellum; 28, Left leg IV.

1.96 (♂, ♀), femur 2.81 (♂), 2.72 (♀), patella 1.95 (♂), 1.80 (♀), chela (with pedicel) 2.96 (♂), 3.00 (♀), chela (without pedicel) 2.73 (♂), 2.76 (♀), hand (without pedicel) 1.16 (♂), 1.31 (♀) times longer than broad, movable finger 1.37 (♂), 1.10 (♀) times longer than hand (without pedicel). Anterior face of femur, and external and internal face of chelal

Figures 29–31.—*Anysrius brochus* new species. 29–30, Male holotype: 29, Genital sternites, ventral; 30, Genitalia, ventral; 31, Genitalia, ventral, female paratype.

hand granulate. Fixed chelal finger with 8 trichobothria, movable chelal finger with 4 trichobothria (Fig. 19); *est, et* and *it* situated in distal portion of fixed finger, *eb, esb, ib, isb* and *ist* situated in basal portion of fixed finger; *isb* situated on internal face of fixed chelal finger; *sb, st* and *t* closely spaced, near middle of movable finger; *t* lanceolate. Chelal teeth contiguous (Fig. 19), fixed finger with 35 (♂), 32 (♀), and movable finger with 38 (♂, ♀) teeth. Chelicera (Figs. 24, 25): hand with 5 setae, movable finger with 1 sub-distal seta; fixed finger with 10 (♂), 15 (♀) teeth on inner surface; movable finger with 12 (♂), 10 (♀) teeth on inner face, dorsal surface of male with 7 lobed processes on external face (Figs. 24, 26); serrula exterior with 25 (♂), 23 (♀) lamellae; flagellum of 6 blades, the 4 distal blades with several anteriorly-directed spinules (Fig. 27); galea of ♂ small and acuminate, of ♀ trifurcate with each ramus terminally trifurcate or bifurcate. Carapace (Fig. 23) with a total of 33 (♂) or 32 (♀) setae, including 4 setae on anterior margin and 8 (♀) or 9 (♂) setae on posterior margin, 1.09 (♂), 1.01 (♀) times longer than broad; 2 small eyes, posterior pair absent. Pleural membrane generally longitudinally striate, although near cephalic region it becomes slightly granulate. Tergal chaetotaxy: ♂, 9: 12: 11: 12: 13: 13: 13: 14: 13: 12: 7: 2; ♀, i1: 10: 11: 12: 11: 13: 14: 13: 12: 12: 6: 2. Sternal chaetotaxy: ♂, 14: (2)15[0](2): (2)15(2): 13: 14: ?: ?: ?: ?: ?: 2; ♀, 5: (2)13(2): (2)10(2): 13: 13: 13: 14: 13: 10: 8: 2. Genital opercula of female not unusual; those of male (Figs. 29) with median cribrate area on sternite II and on sternite IV, sternite II with external lobe. Male genitalia (Fig. 30): lateral apodeme and lateral rod fused for entire length; ejaculatory canal atrium large; median genital sac undivided; genital atrium without internal setae. Female genitalia (Fig. 31) with 1 circular median and 2 small lateral cribriform plates, with very few pores; spermathecae absent. Legs (Fig. 28): moderately stout; leg I with femur 1.44 (♂), 1.07 (♀) times longer than patella; junction between femur I and patella I nearly perpendicular; femur + patella IV 2.93 (♂), 2.72 (♀) times longer than deep; junction between femur IV and patella IV strongly oblique; tibia IV 3.28 (♂), 3.17 (♀) times longer than deep; tibia and metatarsus IV each with single subproximal tactile seta; subterminal tarsal seta acuminate; arolium not divided distally, slightly shorter than claws.

Dimensions (mm), holotype ♂ (paratype ♀): Body length 1.52 (1.63). Pedipalps: trochanter 0.275/0.140 (0.275/0.140), femur 0.435/0.155 (0.435/0.160), patella 0.390/0.200 (0.360/0.200), chela (with pedicel) 0.725/0.245 (0.765/0.255), chela (without pedicel) 0.670 (0.705), hand length (without pedicel) 0.285 (0.335), movable finger length 0.390
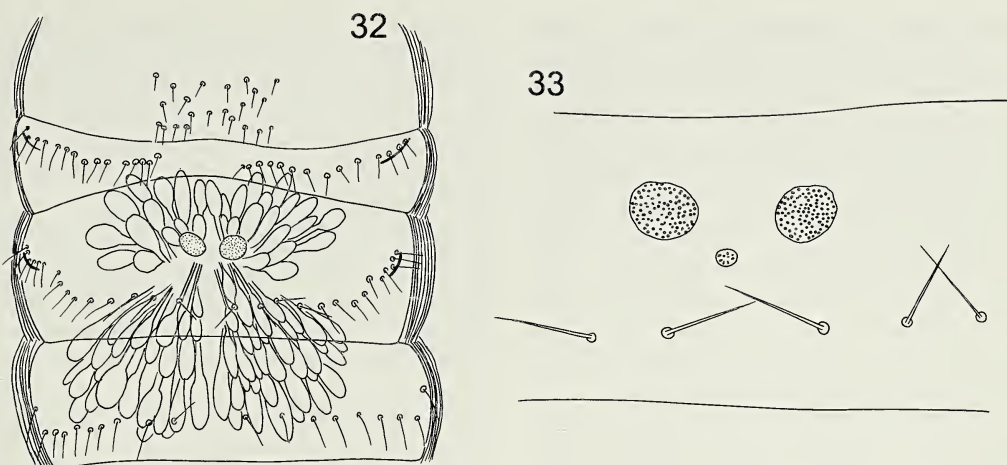
Figures 32–33.—*Syarinus obscurus* (Banks), male from E. of Canjilon, Rio Arriba County, New Mexico, USA; 32, Anterior sternites and glands associated with cribrate areas on sternite IV, ventral; 33, Sternite IV, ventral.

(0.370). Chelicera 0.255/0.125 (0.275/0.145), movable finger length 0.185 (0.200). Carapace 0.445/0.410 (0.415/0.410); diameter of eye 0.025 (0.025. Leg I: femur 0.180/0.090 (0.145/0.100), patella 0.125/0.085 (0.135/0.100), tibia 0.185/0.065 (0.160/0.065), metatarsus 0.080/0.050 (0.085/0.060), tarsus 0.125/0.050 (0.110/0.055). Leg IV: femur + patella 0.410/0.140 (0.395/0.145), tibia 0.295/0.090 (0.285/0.090), metatarsus 0.100/0.065 (0.095/0.070), tarsus 0.160/0.060 (0.145/0.060).

Tritonymph: Pedipalps: trochanter 1.92, femur 2.52, patella 1.87, chela (with pedicel) 2.83, chela (without pedicel) 2.64 times longer than broad. Fixed finger with 7 trichobothria, movable finger with 3 trichobothria (Fig. 20); *eb, esb, est, et, ib, ist, it, b, sb* and *t* present, *t* lanceolate and shorter than other trichobothria. Chelicera: galea trifurcate, each ramus terminally trifurcate; hand with 5 setae, movable finger with 1 seta; fixed finger with 11 teeth, movable finger with 11 teeth; flagellum composed of 6 blades, the 3 distal blades with several anteriorly-directed spinules. Carapace 1.03 times longer than broad; epistome absent; one pair of small eyes present; with 25 setae including 4 setae on anterior margin and 7 setae on posterior margin. Legs as in adult.

Dimensions (mm): Body length 1.455. Pedipalps: trochanter 0.230/0.120, femur 0.340/0.135, patella 0.290/0.155, chela (with pedicel) 0.595/0.210, chela (without pedicel) 0.555, hand length (without pedicel) 0.270,

movable finger length 0.305. Carapace 0.405/0.395.

Deutonymph: Pedipalps: trochanter 1.95, femur 2.57, patella 1.83, chela (with pedicel) 2.84, chela (without pedicel) 2.66 times longer than broad. Fixed finger with 6 trichobothria, movable finger with 2 trichobothria (Fig. 21); *eb, est, et, ib, ist, it, b* and *t* present, *t* lanceolate and slightly shorter than other trichobothria. Chelicera: galea trifurcate, each ramus terminally bifid; hand with 5 setae, movable finger with 1 seta; fixed finger with 7 teeth, movable finger with 8 teeth; flagellum composed of 6 blades, the 4 distal blades with several anteriorly-directed spinules. Carapace 0.94 times longer than broad; epistome absent; one pair of small eyes present; with 22 setae including 4 setae on anterior margin and 6 setae on posterior margin. Legs as in adult.

Dimensions (mm): Body length 1.265. Pedipalps: trochanter 0.185/0.095, femur 0.270/0.105, patella 0.220/0.120, chela (with pedicel) 0.455/0.160, chela (without pedicel) 0.425, hand length (without pedicel) 0.215, movable finger length 0.230. Carapace 0.320/0.340.

Remarks.—*A. brochus* is known only from a single locality in north-western Tasmania.

Syarinus Chamberlin
(Figs. 32–33)

Syarinus Chamberlin 1925: 329; Harvey 1991a: 429 (full synonymy). Type species: *Ideoroncus obscurus* Banks 1893, by original designation.

Diagnosis.—Distinguished from all Syarinidae, except *Anysrius,* by the position of trichobothrium *isb* which is situated on internal face of fixed chelal finger, apex of pedipalpal coxa rounded and with 2 setae, the strongly oblique junction between femur and patella IV, subterminal tarsal seta acuminate, and male sternite IV with median cribrate area (Fig. 33) and associated glands (Fig. 32). *Syarinus* differs from *Anysrius* by male sternite II lacking an external lobe and median cribrate area, and the divided median cribrate area of male sternite IV (Fig. 33).

Description.—Pedipalps: apex of coxa rounded and with 2 setae; chelal fingers curved; chelal teeth contiguous; venom apparatus absent from movable finger; venom duct of fixed finger short. Fixed chelal finger with 8 trichobothria, movable chelal finger with 4 trichobothria; trichobothria *est, et* and *it* situated in distal portion of fixed finger, *eb, esb, ib, isb* and *ist* situated in basal portion of fixed finger; *isb* situated on internal face of fixed chelal finger; *sb, st* and *t* closely spaced near middle of movable finger; *t* lanceolate. Chelicera: hand with 5 (occasionally 6 or 7) setae, movable finger with 1 sub-distal seta; movable finger of ♂ with teeth all grouped distally; flagellum composed of 7 (sometimes 8, but only 6 in *S. strandi*) blades, all but the most basal blade with several anteriorly-directed spinules; galea of ♂ small and usually acuminate, that of ♀ trifurcate with each ramus terminally trifurcate or bifurcate. Carapace: subquadrate, with 1 pair of eyes, anterior eyes small and flat, posterior eyes absent. Pleural membrane generally longitudinally striate. ♂ sternite II without modifications; ♂ sternite IV with divided median cribrate area (Fig. 33) and with associated glands (Fig. 32). Male genital atrium without setae. Female genitalia with 1 median and 2 small lateral cribriform plates, with very few pores; spermathecae absent. Legs: junction between femur and patella I nearly perpendicular; junction between femur and patella IV strongly oblique; metatarsus and tarsus of all legs separate; subterminal tarsal seta acuminate; arolium slightly shorter than claws (except in *S. strandi*).

Material examined.—*Syarinus enhuycki* Muchmore 1968: 3♀, 5 tritonymphs, 3 deutonymphs (all paratypes), E.N. Huyck Preserve, Rensselaerville, Albany County, New York, USA (AMNH, slides).

Syarinus granulatus Chamberlin 1930: 1♀, Cowles, New Mexico, USA (AMNH, S-2161, slide); 2♀, near Sandia Crest, Sandia Mts, Bernalillo County, New Mexico, USA (AMNH, S-1754, S-2145.1, slides); 1♀, 1 tritonymph, Eau Pleine Reserve, Marathon County, Wisconsin, USA (AMNH, S-2364.2, S-2346.7, slides).

Syarinus obscurus (Banks 1893): 1♂, E. of Canjilon, Rio Arriba County, New Mexico, USA (AMNH, S-1911.3, slide); 2♂4♀, Samuel P. Taylor State Park, Marin County, California, USA (FSCA, WM5030); 3♂2♀, Yuba Pass, Sierra County, California, USA (FSCA, WM5037).

Included species.—*Syarinus enhuycki* Muchmore 1968, *S. granulatus* Chamberlin 1930, *S. honestus* Hoff 1956, *S. obscurus* (Banks 1893), *S. palmeni* Kaisila 1964 and *S. strandi* (Ellingsen 1901).

Distribution.—Species of *Syarinus* are generally restricted to montane biotopes in the Holarctic region, but there are lowland records from more northern latitudes. Of the montane species, *S. enhuycki* is found in the northern parts of the Appalachian Mountains (Muchmore 1968), with outlying populations in Michigan (Nelson 1975) and possibly Wisconsin, based upon a single collection identified as *S. granulatus* by Hoff & Bolsterli (1956) (see Muchmore 1968). Three species are mostly restricted to the Rocky Mountains: *S. honestus,* which is known from a single locality in New Mexico at 10,250 ft (=3124 m) (Hoff 1956); *S. granulatus,* which has been reliably recorded only from Colorado (Chamberlin 1930) and New Mexico (Hoff 1956); and *S. obscurus* which has been recorded from Canada (British Columbia, Saskatchewan) and USA (California, Montana, New Mexico, Utah, Washington, Wyoming) (see Harvey 1991a). Of the remaining two species, *S. palmeni* is known only from a single locality in Newfoundland (Kaisila 1964), and *S. strandi* has been taken from six different localities in northern Europe (Austria, Finland, Norway and Germany). Muchmore (1990) also records members of the genus from Minnesota, Oregon and Ontario.

Remarks.—*Syarinus,* the type genus of the Syarinidae, is currently known only from North America and northern Europe. It has been diagnosed by Chamberlin (1930) and Hoff (1956), and good descriptions of new or previously poorly known species were provided by Chamberlin (1930), Hoff (1956), Kais-

ila (1964), Muchmore (1968), Mahnert (1976), Schawaller (1987) and Schmarda (1997). Although males appear to be relatively rare in museum collections, it is somewhat surprising that the peculiar morphology of the male sternite IV described and illustrated here has not been noticed by previous authors. The discovery of two or more cribrate areas on sternite IV and associated glands on males of at least three species of *Syarinus* raises the possibility that this character state is present in all species of the genus. However, I have not had the opportunity to examine males of *S. granulatus, S. strandi* and *S. palmeni,* and any discussion on the distribution of this character state must await a more detailed review of all species attributed to the genus. In addition, it appears that males of *Syarinus* species share another unique feature, whereby the teeth of the movable cheliceral finger are grouped near the level of the galeal seta in *S. granulatus, S. honestus, S. obscurus* and *S. enhuycki* (e.g., Chamberlin 1931, fig. 13M; Hoff 1956: 11, 15; Muchmore 1968: 113). Once again, the utility of this feature will remain unknown until males of *S. palmeni* and *S. strandi* are more fully described.

DISCUSSION

Morphology.—Some of the features that occur in species of *Anysrius* and at least some species of *Syarinus* are of extreme interest and occur nowhere else in the Pseudoscorpiones.

The dorsal 'teeth' on the movable cheliceral finger of male *A. brochus* are unparalleled within the order, as are the specialized blunt setae on the pedipalpal patella of male *A. chamberlini.* The modifications of sternite II of male *Anysrius* species, with an external lobe and cribrate area, are similarly unique to this genus. The cribrate area of sternite IV is restricted to *Anysrius* spp. as well as to males of *S. obscurus* and *S. honestus* (Harvey pers. obs.) and *S. enhuycki* (W.B. Muchmore *in litt.*), but in the two *Syarinus* species examined the cribrate area is divided into two, or rarely three, separate regions (Fig. 33) whereas it is a single region in *Anysrius* spp. (Figs. 16, 29). The nature of sternite IV has not been ascertained for the remaining species of *Syarinus* (*S. granulatus, S. palmeni* and *S. strandi*) and males must be reexamined to determine whether they can be retained in the genus *Syarinus,* since the lack of this character state

requires that any species concerned would probably need to be placed in a new genus situated as the sister-group to the *Anysrius* + *Syarinus* clade.

The cribrate area of sternite IV in *Syarinus* is associated with a large number of glands, all apparently discharging via the cribrate area (Fig. 32). Despite close examination of males of *A. chamberlini* and *A. brochus,* a similar glandular system could not be detected in the Tasmanian forms.

Abdominal modifications are known in other syarinid genera, but these take on quite different forms and are not considered homologous with the features found in *Syarinus* and *Anysrius.* These include the gland openings found on sternite VI in some males of *Chitrella* and *Pseudoblothrus* (e.g., Chamberlin 1931; Vachon 1954), and the small circular structures suspected to be glandular pores situated in the intersegmental membranes of *Pseudoblothrus peyerimhoffi* (Simon 1905) and *P. strinatii* Vachon 1954 (Vachon 1952, 1954).

Biogeography.—The occurrence of related syarinid genera in Tasmania, North America and northern Europe, without any potentially related genus occurring in the intervening tropical latitudes, can only be explained by one of two hypotheses: dispersal or vicariance. The dispersal model requires a rigid set of conditions which would be extremely demanding upon an organism as small and relatively immobile as a pseudoscorpion which prefers temperate forest litter. The ancestor to either *Anysrius* or *Syarinus* would have dispersed across one or more large expanses of water, the Pacific Ocean, to colonize Tasmania from the Holarctic zone, or vice versa. While some pseudoscorpions, including *Syarinus* (see Kaisila 1949; Muchmore 1971), exhibit phoretic behavior, whereby they attach themselves to flying insects, which may result in dispersal, it seems unlikely that large-scale ocean crossings are possible or are likely to result in successful breeding amongst conspecifics after the colonizing event has occurred. If this scenario were possible, a wider distribution of the Tasmanian species would seem likely. Despite the examination of numerous Tasmanian pseudoscorpions over the past 20 years, I have not encountered any material from outside of the two localities listed above. In addition, representatives of neither of these

syarinid genera have been found in interven- ing areas, despite the examination of thousands of pseudoscorpions from Australia and nearby areas, including the islands of the southwest Pacific, by the author.

Therefore, the remaining hypothesis, that the modern distribution is the result of vicar- iance events dating back to the Mesozoic (ca. 170 million ybp) when Pangea was still intact (Smith et al. 1994), is the preferred scenario. As argued by numerous different authors studying relatively immobile organisms (e.g., Brundin 1966; Platnick 1975), the most par- simonious explanation for such distribution patterns involves the rejection of a dispersalist model and the acceptance of the great age of these clades of organisms which predate the geological movements of the continents which now separate them.

An identical scenario must be evoked for the Pseudogarypidae, which have a remark- ably similar distribution pattern to that of the *Syarinus-Anysrius* clade (Recent species in Tasmania and North America, with three Ter- tiary species recorded from European Baltic Amber). These Pangean clades of pseudoscor- pions with distinct bipolar distributions are quite rare and serve to illustrate that the com- mon ancestor to the *Syarinus-Anysrius* clade must have evolved prior to the breakup of Pangea during the Mesozoic.

ACKNOWLEDGMENTS

LITERATURE CITED

Anonymous. 1996. Report of the Nomenclature Committee. Arachnologia, 13:5.

Banks, N. 1893. New Chernetidae from the United States. Canadian Entomol., 25:64–67.

Brundin, L. 1966. Transantarctic relationships and their significance as evidenced by chironomid midges with a monograph of the subfamilies Po- donominae and Aphroteniinae and the austral Heptagyiae. K. Svenska Vetensk. Handl., 11:1– 472.

Chamberlin, J.C. 1925. On a collection of pseu- doscorpions from the stomach contents of toads. Univ. California Publ. Entomol., 3:327–332.

Chamberlin, J.C. 1930. A synoptic classification of the false scorpions or chela-spinners, with a re- port on a cosmopolitan collection of the same. Part II. The Diplosphyronida (Arachnida-Chelo- nethida). Ann. Mag. Nat. Hist., (10)5:1–48, 585– 620.

Chamberlin, J.C. 1931. The arachnid order Che- lonethida. Stanford Univ. Publ., Biol. Sci., 7(1): 1–284.

Ellingsen, E. 1901. Sur une espèce nouvelle d'*Ideobisium* genre des pseudoscorpions de l'Europe. Bull. Soc. Zool. France 26:86–89.

Harvey, M.S. 1990. Trichobothrial "migration" in diplosphyronid pseudoscorpions. Acta Zool. Fennica, 190:157–160.

Harvey, M.S. 1991a. Catalogue of the Pseudoscor- pionida. Manchester Univ. Press, Manchester. vi + 726 pp.

Harvey, M.S. 1991b. The cavernicolous pseudo- scorpions (Chelicerata: Pseudoscorpionida) of Cape Range, Western Australia. Rec. Western Australian Mus., 15:487–502.

Harvey, M.S. 1992. The phylogeny and classifi- cation of the Pseudoscorpionida (Chelicerata: Arachnida). Invert. Taxon., 6:1373–1435.

Harvey, M.S. 1996. The biogeography of Gond- wanan pseudoscorpions. Rev. Suisse Zool., hors serie, 1:255–264.

Hoff, C.C. 1956. Diplosphyronid pseudoscorpions from New Mexico. American Mus. Novit., 1780: 1–49.

Hoff, C.C. & J.E. Bolsterli. 1956. Pseudoscorpions of the Mississippi River drainage basin area. Trans. American Micro. Soc., 75:155–179.

Kaisila, J. 1964. Some pseudoscorpionids from Newfoundland. Ann. Zool. Fennici, 1:52–54.

Mahnert, V. 1976. Zur Kenntnis der Gattungen *Acanthocreagris* und *Roncocreagris* (Arachnida, Pseudoscorpiones, Neobisiidae). Rev. Suisse Zool., 83:193–214.

Mahnert, V. 1985. Weitere Pseudoskorpione (Arachnida) aus dem zentralen Amazonasgebiet (Brasilien). Amazoniana, 9:215–241.

Muchmore, W.B. 1968. A new species of the pseu- doscorpion genus *Syarinus* (Arachnida, Chelo- nethida, Syarinidae) from the northeastern Unit- ed States. J. New York Entomol. Soc., 76:112– 116.

Muchmore, W.B. 1971. Phoresy by North and Cen- tral American pseudoscorpions. Proc. Rochester Acad. Sci., 12:79–97.

Muchmore, W.B. 1982a. Pseudoscorpionida. Vol.

2, Pp. 96–102. *In* Synopsis and Classification of Living Organisms. (S.P. Parker, ed.). McGraw-Hill, New York.

Muchmore, W.B. 1982b. The genera *Ideobisium* and *Ideoblothrus,* with remarks on the family Syarinidae (Pseudoscorpionida). J. Arachnol., 10:193–221.

Muchmore, W.B. 1990. Pseudoscorpionida. Pp. 503–527. *In* Soil Biology Guide. (D.L. Dindal, ed.). John Wiley & Sons, New York.

Muchmore, W.B. 1996. A remarkable new genus and species of Pseudoscorpionida (Syarinidae) from a cave in Arizona. Southwest. Nat., 41: 145–148.

Nelson, S., Jr. 1975. A systematic study of Michigan Pseudoscorpionida (Arachnida). American Midl. Nat., 93:257–301.

Platnick, N.I. 1975. Drifting spiders or continents?: vicariance biogeography of the spider subfamily Laroniinae (Araneae: Gnaphosidae). Syst. Zool., 25:101–109.

Schawaller, W. 1987. Erstnachweis der Familie Syarinidae in Deutschland: ein Reliktvorkommen von *Syarinus strandi* im Oberen Donautal (Arachnida: Pseudoscorpiones). Jahr. Gesell. Naturk. Württemberg, 142:287–292.

Schmarda, T. 1997. Erstnachweis von *Syarinus strandi* (Ellingsen 1901) in Tirol/Österreich (Arachnida, Pseudoscorpiones, Syarinidae). Ber. Naturwiss.-Med. Ver. Innsbruck, 84:105–109.

Smith, A.G., D.G. Smith & B.M. Funnell. 1994. Atlas of Cenozoic and Mesozoic Coastlines. Cambridge Univ. Press, Cambridge. 99 pp.

Vachon, M. 1952. Remarques préliminaires sur l'anatomie et la biologie de deux Pseudoscorpions très rare de la faune française: *Pseudoblothrus peyerimhoffi* (E. S.) et *Apocheiridium ferum* (E. S.). Bull. Mus. Nat. Hist. Nat., Paris, (2)24:536–539.

Vachon, M. 1954. Remarques morphologiques et anatomiques sur les Pseudoscorpions (Arachnides) appartenant au genre *Pseudoblothrus* (Beier) (Fam. Syarinidae J.C.C.) (à propos de la description de *P. strinatii* n. sp., des cavernes de Suisse). Bull. Mus. Nat. d'Hist. Nat., Paris, (2) 26:212–219.

PSEUDOSCORPIONS OF THE GENUS *RHOPALOCHERNES* (CHERNETIDAE) FROM PANAMA AND VENEZUELA

Jacqueline Heurtault: Muséum national d'Histoire naturelle, Laboratoire de Zoologie (Arthropodes), 61 rue de Buffon, 75005 Paris, France

ABSTRACT.   *Rhopalochernes panamensis* new species is described from a palm tree in the Canal Zone of Panama. *Rhopalochernes chamberlini* new species is described from Pueblo Cuyagua Venezuela. The problems encountered in assigning these species to either *Rhopalochernes* or *Pseudopilanus* are briefly discussed. An unusual anomaly, involving the loss of trichobothria from the both the fixed and movable fingers of a single chela, is described in *R. panamensis.*

The two pseudoscorpions reported here are of interest due to the problems posed in their generic assignment. They show characteristics of both *Rhopalochernes* and *Pseudopilanus.* The first was found in Venezuela by C. Bordon and V. Decu, while the second was collected by the author in Panama. The specimens are mounted on slides and deposited in the Laboratoire de Zoologie (Arthropodes) of the Muséum national d'Histoire naturelle, Paris.

Rhopalochernes chamberlini new species
(Figs. 1–7)

Type.—Holotype female, Venezuela, Pueblo Cuyagua, 18 December 1987, C. Bordon and V. Decu.

Etymology.—This species is named for J.C. Chamberlin, in recognition of his contributions to pseudoscorpion systematics.

Description.—*Female* (male unknown): Carapace and pedipalps moderately sclerotized, reddish brown in color, abdomen and legs yellowish brown. Surface of carapace, tergites and palps granulate, with broad, foliate-serrate vestitural setae. Carapace with two transverse furrows and one pair of eyespots; chaetotaxy 29–16–8 (53), with 6 setae along anterior margin and 8 along posterior margin.

Tergites 1–10 and sternites 4–10 divided. Pleural membrane longitudinally plicate and rugose. Tergal chaetotaxy: 10–12–13–15–15–16–14–12–12–8–2, tergites 4–11 with 1 lateral and (less distinctly) 1 discal seta. All ventral setae acuminate. Anterior genital operculum with 13 setae; posterior operculum with 6 setae along posterior margin (Fig. 1). Spermathecae in form of 2 sacs (Fig. 2); ducts indistinct, but apparently separate. Chaetotaxy of remaining sternites: 4–7–15–14–14–12–10–9–T2T–2.

Chelicera: hand with 4 acuminate setae, flagellum with 3 blades, distal blade larger and strongly dentate along distal margin, 2 basal blades short and lying close together; galea with 6 denticles (Fig. 4).

Palps (Figs. 5–7): Stout; moderately granulate on inner and exterior margins, relatively smooth dorsally and ventrally. Some setae dentate at base of fingers. Femur 2.6× as long as broad, tibia 2.4× as long as broad, chela (without pedicel) 3.2× as long as broad and hand (with pedicel) 0.9× as long as movable finger. Trichobothria distributed as shown in Fig. 5. Fixed finger with one internal accessory tooth near tip and about 40–43 ordinary teeth; movable finger without accessory teeth. Venom apparatus developed in movable finger only, *nodus ramosus* in middle of finger, slightly proximad of *st.*

Legs granulate, setae feathered on external margins and dentate on internal margins; legs III–IV with a short tactile seta on coxa, femur and tarsus (Fig. 3).

Measurements (in mm). Body length: 1.42; Carapace: 0.49/0.46; palpal femur: 0.38/0.14; tibia: 0.36/0.15; hand with pedicel: 0.31/0.20; movable finger: 0.33; chela (with pedicel) 0.65/0.20 (length without pedicel 0.61); Leg IV, femur: 0.28/0.075; tibia: 0.26/0.067; tarsus: 0.21/0.052.

Remarks.—This species can be assigned to the genus *Rhopalochernes* Beier 1932, by virtue of the 3-bladed flagellum and the presence of a short tactile seta on tarsus IV and tergite
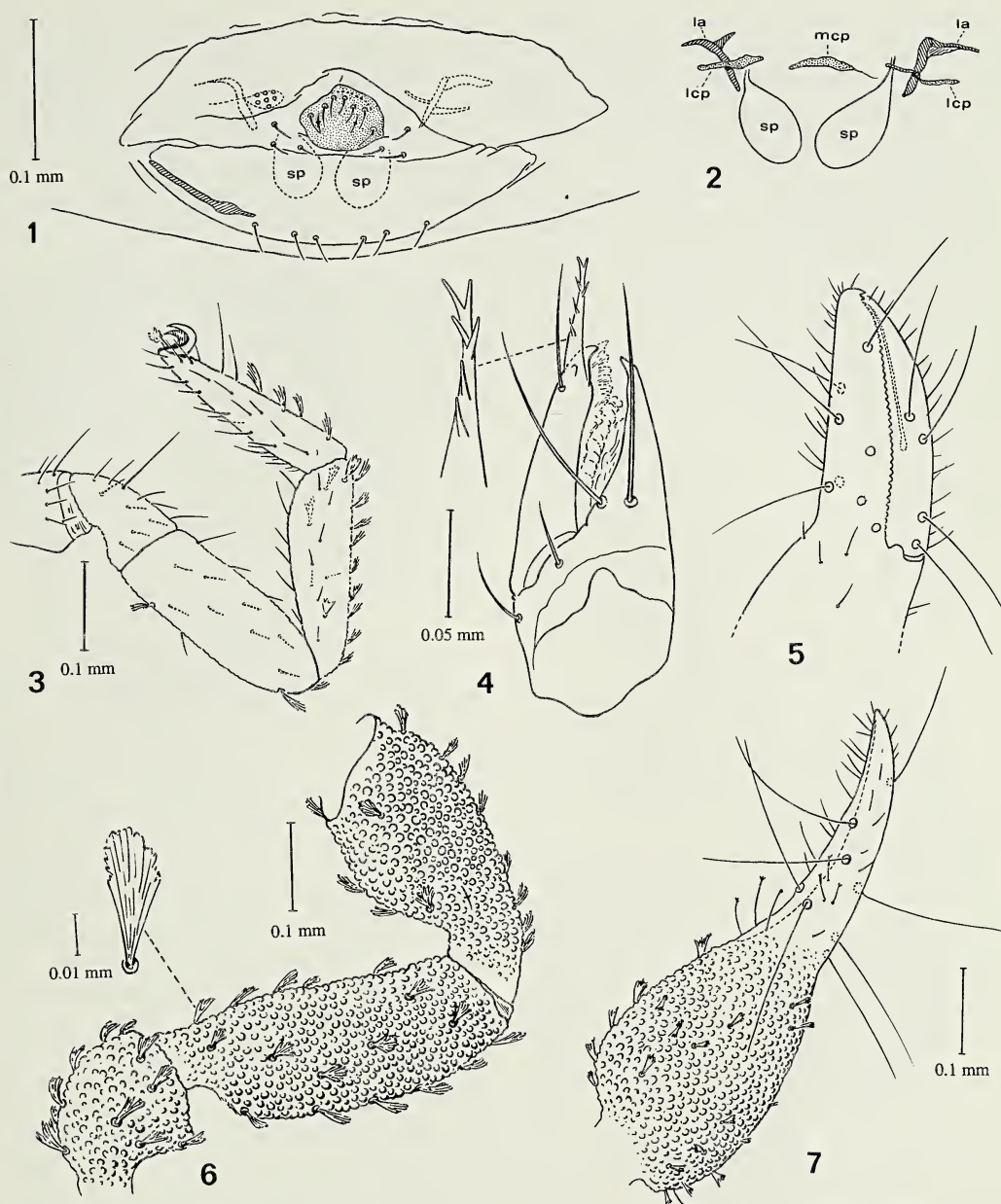
Figures 1–7.—***Rhopalochernes chamberlini*** new species, holotype female. 1, Ventral view of genital region; 2, Ventral view of genitalia (*sp:* spermatheca, *mcp:* median cribriform plate, *lcp:* lateral cribriform plate, *la:* lateral apodeme); 3, Left leg IV; 4, Left chelicera with detail of the galea; 5, Right chela showing trichobothria, *nodus ramosus* and primary duct of venom apparatus; 6, 7, Right palp, showing structure of tegument and leaf-like setae.

XI. It is similar to *R. antillarum* (With 1908), but differs in being smaller and less robust (e.g., femur 0.44 mm long, ratio 2.6 in *antillarum,* according to With 1908) and in having the finger of the chela only slightly longer than the hand (distinctly longer in *antillarum*).

Rhopalochernes panamensis new species
(Figs. 8–13)

Type.—Holotype female, Panama, Canal Zone, Madden Forest Reserve, Palmera del Corozo, August 1983, in organic debris at base of sheathed leaf axils of palm, *Schiela-*

zonensis sp., J. Heurtault. This restricted biotope, situated 1–2 m above the ground, harbored other groups characteristic of the soil fauna, including Acari, Collembola, Amblypygi and the scorpion *Opisthacanthus lepturus* (Palisot de Beauvois 1805).

Description.—*Female* (male unknown): Carapace and pedipalps moderately sclerotized, light brown in color, abdomen and legs yellowish brown. Surface of carapace, tergites and palps granulate, with broad, foliate vestitural setae. Carapace with two transverse furrows and one pair of eyespots; chaetotaxy 29–16–9 (54), with six setae on anterior margin and 9 on posterior. Tergites 1–10 and sternites 4–10 divided. Pleural membranes longitudinally plicate and rugose. All ventral setae acuminate. Tergal chaetotaxy: 10–11–10–15–14–15–13–13–9–11–10–2. Anterior genital operculum with 10 setae, posterior operculum with 6 setae; chaetotaxy of remaining sternites: 6–9–13–14–12–10–8–T2T–2. Spermathecae not visible in slide-mounted specimen.

Chelicera (Fig. 9): Hand with 4 acuminate setae; flagellum of 3 blades, distal blade serrate, 2 basal blades simple and close to larger distal blade; galea with 6 rami. Serrula exterior with 14 or 15 lamellae. One isolated tooth near base of galeal seta.

Palps (Figs. 11–13): All surfaces granulate; short, leaf-like setae on the interior margin of the hand, denticulate setae on exterior margin. Venom apparatus developed in movable finger only, with *nodus ramosus* between *t* and *st.* Fixed finger with 4 accessory teeth; movable finger without accessory tooth; ordinary teeth numbering about 39 on each finger. Normal distribution of trichobothria as shown in Fig. 11. Femur 2.5× as long as broad, tibia 2.3× as long as broad, chela (without pedicel) 3.0× as long as broad and hand (including pedicel) 0.8× as long as movable finger.

Coxa, femur and tarsus of legs III–IV with a short tactile seta (Fig. 10).

Measurements (in mm). Body length: 1.14; Carapace: 0.45/0.41; palpal femur: 0.32/0.13; tibia: 0.31/0.14; hand (with pedicel): 0.29/0.19; movable finger: 0.34; chela (with pedicel): 0.60/0.19 (length without pedicel 0.57); Leg IV, femur: 0.33/0.10; tibia: 0.27/0.06; tarsus: 0.24/0.04.

Remarks.—Like *Rhopalochernes chamberlini*, *R. panamensis* can be placed in the genus *Rhopalochernes* by virtue of the 3-bladed flagellum and the presence of a short tactile seta on tarsus IV and tergite XI. It differs from the other species of the genus by its very small size. The generic placement of this species (and *R. chamberlini*) is provisional, pending more information on the form of the spermathecae and other important characters in species of *Rhopalochernes* and *Pseudopilanus.*

The holotype of *R. panamensis* shows an interesting anomaly in the number of trichobothria on the right chela: *ist* is missing from the fixed finger and *t* and *st* missing from the movable finger (Fig. 12). The right chela is otherwise normal and similar to the left chela (which has the normal number of trichobothria). While it is not rare to encounter anomalies on one finger or the other, it is unusual to find trichobothria missing from both fingers of a single chela.

DISCUSSION

The genus *Rhopalochernes* Beier 1932 was established by Beier (1932), with *Chelifer ohausi* Tullgren 1907 as the type species. Although Tullgren (1907) described the genital area of the male as being of the 'Chelifer subruber type', Beier placed the new genus in the Chernetidae. A recent re-examination of two syntypes (1♂, 1♀, in Zoologishes Museum, Hamburg) confirms that they are indeed chernetids. Glandular setae are absent on the sternites and a venom duct is only present in the movable finger (*nodus ramosus* proximad of *t*). The accessory teeth are reduced to just two, situated on the external face of the fixed chelal finger. A short tactile seta is present distally on the tarsus of leg IV and two tactile setae are present on tergite XI. The spermathecae have the same general form as those illustrated for *R. chamberlini,* consisting of a pair of oval sacs with moderately long ducts that are close, but separate, at their base.

Beier (1957) later created the new genus *Pseudopilanus* Beier 1957 for *Pseudopilanus fernandezianus* Beier 1957, which was described from a single tritonymph and compared with the African genus *Pilanus* Beier 1930. According to the original diagnoses, *Pseudopilanus* differed from *Rhopalochernes* in lacking accessory teeth on the fingers and by the absence of a tactile seta on the tarsus of leg IV. However, Beier (1959) transferred the species *echinatus* Ellingsen 1904 from
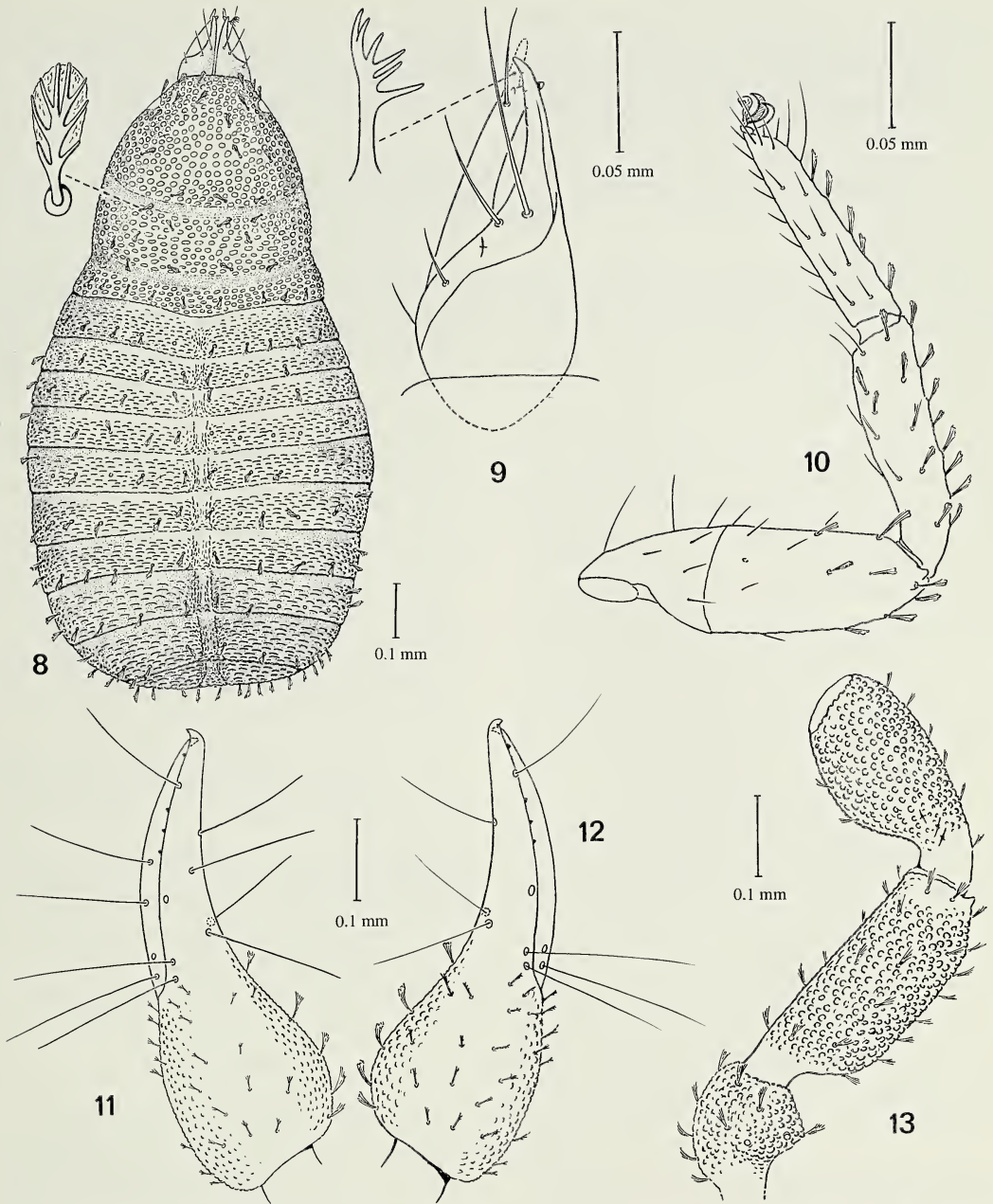
Figures 8–13.——**Rhopalochernes panamensis** new species, holotype female. 8, Habitus, with detail of leaf-like seta; 9, Left chelicera, with detail of galea; 10, Right leg IV; 11, Left chela; 12, Right chela with abnormal trichobothriotaxy; 13, Right palp, minus chela.

Rhopalochernes to *Pseudopilanus,* based on the absence of a tactile seta on the tarsus of leg IV and the arrangement of the trichobothria. The close relationship between these two genera was explicitly recognized by Beier (1964), who considered that they could be distinguished by the positions of trichobothria *et*

and *it.* However, this character is probably only of specific value (Mahnert 1985).

Beier's (1977) description of *Pseudopilanus inermis* Beier 1977, from the Galapagos, includes the following characters: hand of chelicera with 7 setae; fingers of chela as long as hand (minus pedicel) and without accessory

teeth; tergite 11 and tarsus of leg IV without tactile setae. In noting that *P. inermis* is closely related to "*P. foliosus* (Balzan)", Beier effectively transferred *R. foliosus* to the genus *Pseudopilanus* (though this combination is not given by Harvey 1991). This paper is particularly interesting because it shows Beier's uncertainty regarding his genera *Rhopalochernes* and *Pseudopilanus*.

Thus, over the course of successive papers, the characters used to distinguish the two genera were reduced to one, namely the presence or absence of accessory teeth. Part of the difficulty in separating these two genera lies in the subjectivity of characters such as the presence or absence of tactile setae. The two species described here are of interest because they are evidently closely related, despite the fact that the accessory teeth of *R. chamberlini* are greatly reduced, as in *R. ohausi*. Thus it would seem that the presence or absence of accessory teeth is not a valid character for separating *Rhopalochernes* from *Pseudopilanus*. The problem of the validity of *Pseudopilanus* cannot, however, be resolved until the adults of the type species are known.

ACKNOWLEDGMENTS

LITERATURE CITED

Beier, M. 1932. Pseudoscorpionidea II. Subord. C. Cheliferinea. Tierreich, 58:1–294.

Beier, M. 1957. Los insectos de las Islas Juan Fernandez. 37. Die Pseudoscorpioniden-Fauna der Juan-Fernandez-Inseln (Arachnida, Pseudoscorpionida). Rev. Chilena Entomol., 5:451–464.

Beier, M. 1959. Zur Kenntnis der Pseudoscorpioniden-Fauna des Andengebietes. Beitr. z. Neotropischen Fauna, 1 (3):185–228.

Beier, M. 1964. Die Pseudoscorpioniden-Fauna Chiles. Ann. Naturhist. Mus. Wien, 67:307–375.

Beier, M. 1977. Pseudoscorpionidea. *In* Mission Zoologique Belge aux îles Galapagos et en Ecuador (N. et J. Leleup 1964–1965), 3:92–112.

Harvey, M. 1991. Catalogue of the Pseudoscorpionida. Manchester Univ. Press, Manchester.

Mahnert, V. 1985. Weitere Pseudoskorpione (Arachnida) aus dem zentralen Amazonasgebiet (Brasilien). Amazoniana, 9 (2):215–241.

Tullgren, A. 1907. Zur Kenntnis aussereuropäischer Chelonethiden des Naturhistorischen Museums in Hamburg. Mitt. Naturhist. Mus. Hamburg, 24:21–75.

With, C.J. 1908. An account of the South American Cheliferinae in the collections of the British and Copenhagen Museums. Trans. Zool. Soc. London, 18:217–340.

A NEW SPECIES OF *XENOCHELIFER* WITH COMMENTS ON THE GENUS (PSEUDOSCORPIONIDA, CHELIFERIDAE)

William B. Muchmore: Department of Biology, University of Rochester, Box 270211, Rochester, New York 14627-0211 USA

ABSTRACT.   A new species, *Xenochelifer derhami,* is described from Inyo County, California. It differs from *X. davidi* Chamberlin primarily in having three, rather than two, trichobothria on the movable chelal finger. The generic diagnosis is revised accordingly. It is shown that *Xenochelifer* Chamberlin is closely allied to *Hysterochelifer* Chamberlin.

In 1949, J.C. Chamberlin defined a new genus, *Xenochelifer,* based on the newly described species, *Xenochelifer davidi,* from southern California. No further material of *X. davidi* has been discovered, and no other related species has been recognized until now. I here describe a new species which certainly is congeneric with *X. davidi,* but which possesses some characters necessitating a slight revision of the generic diagnosis.

METHODS

The following abbreviations are used in the text. L = length; L/B = ratio, length/breadth; L/D = ratio, length/depth; T = tactile seta. Specimens are deposited in the California Academy of Sciences, San Francisco, California (CAS), the Florida State Collection of Arthropods, Gainesville, Florida (FSCA), and the Muséum National d'Histoire Naturelle, Paris (MNHN).

SYSTEMATICS

Xenochelifer Chamberlin 1949

Xenochelifer Chamberlin 1949:10; Muchmore 1990:524; Harvey 1991:533.
Type species. - *Xenochelifer davidi* Chamberlin 1949.
Type locality. - Big Rock Creek, Los Angeles County, California.

Diagnosis (revised).—The diagnosis presented by Chamberlin (1949:10–12) is quite detailed and covers most features of the genus, based on the single species, *Xenochelifer davidi.* With the recognition of a second species, the following revisions and additions can be made. The movable finger of the palpal chela is distinctly shorter than the hand and bears only two or three trichobothria — *st,* and sometimes *sb,* missing from the normal complement. An accessory seta may occasionally occur on the cheliceral hand, similar in size and shape to *bs* and *sbs.* Guard setae on anterior margin of sternite 3 of the male (posterior genital operculum) curved distally and with a strong lateral spine.

Comments.—Chamberlin (1949) did not compare the new genus *Xenochelifer* with any other cheliferids, except to point out that it differs from all of them in the reduced chaetotaxy of the chela. In the light of our present knowledge, it can be seen that *Xenochelifer* is closely related to *Hysterochelifer* Chamberlin (1932:19). Unfortunately, *Chelifer fuscipes* Banks 1909 from California, the type species of *Hysterochelifer,* is poorly known and the genus is not defined satisfactorily (see Hoff 1956:10). Benedict & Malcolm (1979) stated that a revision of the western [USA] species of *Hysterochelifer* was forthcoming, but that has not appeared, and still no adequate description of *Chelifer fuscipes* has been published.

Possibly the most reliable diagnosis of *Hysterochelifer* presently available is that of Hoff (1956:10), which is based on the three recognized American species. [Beier's most recent diagnosis (1963:283) was probably based on European species, which may or may not be congeneric with *H. fuscipes.*] *Xenochelifer* agrees with *Hysterochelifer* in all of the diagnostic characters mentioned by Hoff, except that it always has five or more (rather than four or five) setae on the cheliceral hand and has only two or three (rather than four) trichobothria on the movable chelal finger. In ad-
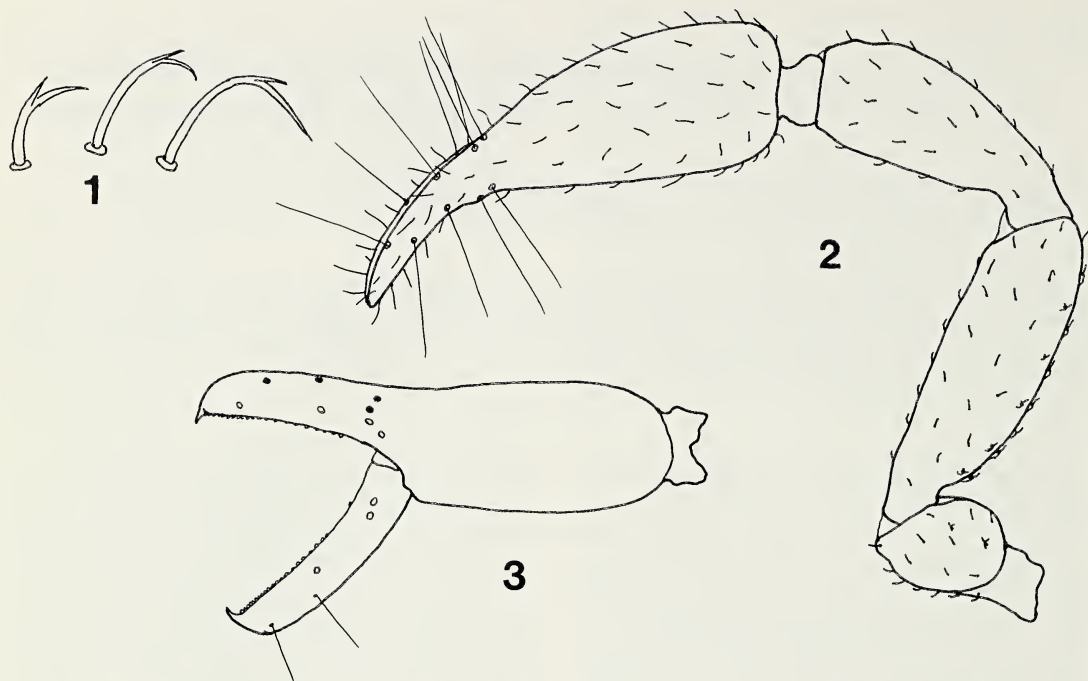
Figures 1–3.—*Xenochelifer derhami* new species, holotype male. 1, Setae from anterior margin of sternite 3 (posterior genital operculum); 2, Right palp, dorsal view; 3, Left chela, lateral view; most setae omitted, only the two pseudotactile setae on movable finger shown; darkened trichobothrial areoles are underneath.

dition, the two genera are similar in the possession of curved, spinous setae on the anterior margin of sternite 3 (posterior genital operculum) in the male, and of two slender pseudotactile setae on the movable finger of the palpal chela. In Muchmore's (1990) key to the pseudoscorpions of North America north of Mexico, representatives of *Xenochelifer* would key out to *Hysterochelifer* except for the reduced number of trichobothria on the movable chelal finger. *Xenochelifer* also differs from *Hysterochelifer* in having more robust palps.

So many are the similarities between *Xenochelifer* and *Hysterochelifer* as presently defined that, despite the reduction in number of trichobothria and other less distinctive differences, the former might be considered a synonym of the latter. However, it seems best to maintain *Xenochelifer* as a separate genus until more is learned about *Hysterochelifer*.

Xenochelifer davidi Chamberlin

Xenochelifer davidi Chamberlin 1949:12–17, figs. 4A-E, 5A-P; Hoff 1958:33; Harvey 1991:533.

Material examined.—One male and one female paratypes (JC-552.04001, 2) from Big Rock Creek, Los Angeles County, California, under cottonwood bark, 25 April 1926 (J.C. Chamberlin), mounted on slides, in CAS; one female paratype (JC-492.01001) from "Sud California (Morr. 81) (5.914), L. Fage Collection", mounted on slide, in MNHN.

Comments.—Chamberlin's very detailed description of this species makes it unmistakable. However, no further material has become available (probably because of insufficient collecting in suitable habitats).

Xenochelifer derhami new species
Figs. 1–3

Type material.—Holotype male (WM63-55.02001), allotype female (WM635-5.02002), and one male, one female paratypes from Big Pine, Inyo County, California, 1220 m elevation, "ant association," June 1981 (D. Giuliani); one female paratype from same locality, August 1979 (D. Giuliani). All mounted on slides, in FSCA.

Diagnosis.—Similar in most respects to

Xenochelifer davidi Chamberlin, but a little larger (palpal femur L 0.85–0.96 versus 0.71–0.825), with more slender appendages (L/B of chela of male 3.35–3.5 versus 2.85–2.95), and with three rather than two trichobothria on movable finger of chela.

Description.—*Male:* Generally like *X. davidi,* with the following particular features. Carapace and palps reddish brown, other parts lighter. Carapace about as long as broad; surface heavily granulate, with a few low tubercles laterally; two shallow transverse furrows; a small crest at each posterolateral corner; two large corneate eyes; about 110 short setae, slightly clavate, terminally denticulate. Coxal area generally typical of Cheliferidae; coxa IV with a prominent lateral spur; coxal sacs present, without atria, a little larger than in *X. davidi.* Abdominal tergites 2–10 and sternites 4–10 divided; surfaces of tergites and sternites scaly; tergites 1–9 with lateral crests, large anteriorly, smaller posteriorly; pleural membranes longitudinally striate; most dorsal setae clavodentate, most ventral setae acuminate. Tergal chaetotaxy of holotype 16: 17: 17: 18: 20: 22: 21: 20: 20: 18: 16: 2; sternal chaetotaxy of holotype 80: [2–2]: (0)19(0): (1)15(1): 19: 19: 17: 15: 14: 14: 3T4T3: 2; paratypes similar. Setae on both tergites and sternites tend to be biseriate laterally, especially toward posterior end. Internal genitalia essentially as illustrated by Chamberlin for *X. davidi* (1949: fig. 5D). Guard setae on anterior margin of sternite 3 ([2–2] in holotype and [5–3] in paratype) strongly curved and with a distinct spine (Fig. 1); other setae on anterior sternites acuminate, including those of sternite 2. Chelicera 0.33 as long as carapace; hand with five setae, *bs* and *sbs* short, denticulate, *es* long, acuminate; flagellum of three setae, the distal one sparsely denticulate; serrula exterior of 17 blades; galea short, with 3–4 small, terminal rami. Palp (Fig. 2) more slender than that of *X. davidi;* L/B of trochanter 1.65, femur 3.25–3.3, patella 2.55–2.65, and chela (without pedicel) 3.35–3.5; L/D of hand (without pedicel) 2.15–2.25; movable finger L / hand L 0.88–0.92. Surfaces heavily granulate, except chelal fingers; most setae short, clavodentate; femur with scattered setiferous tubercles. Trichobothriotaxy as shown in Fig. 3; fixed finger with the usual eight trichobothria, movable finger with three; positioned as in *X. davidi,* but with the addition of *sb* on movable finger.

Two pseudotactile setae on movable finger as described by Chamberlin for *X. davidi* (see 1949: fig. 4E). Fixed finger with 23 and movable finger with 22–24 cusped teeth, lower and slightly spaced proximally. Venedens well developed in both fingers, but venom ducts not apparent. Legs rather slender; surfaces granulate, femur + patella IV with few setiferous tubercles; claws not dentate; subterminal tarsal setae curved, usually with a small spine. Leg I: tarsus swollen distally, with prominent terminal spine and modified claws, very much like that of *X. davidi* (Chamberlin 1949: figs. 5L-N). Leg IV: L/D of femur + patella 3.0, tibia 3.75, and tarsus 3.8; moderately long tactile seta nearly at distal end of dorsal margin.

Female: Much like male but with the following particular features. One paratype is apparently teneral, and very light in color. Carapace heavily granulate, but with less distinct tubercles and without posterolateral crests. Abdominal tergites without lateral crests, otherwise similar to those of male. Coxal area unmodified. Tergal chaetotaxy of allotype 14: 17: 16: 18: 24: 25: 24: 23: 23: 20: 18: 2; sternal chaetotaxy of allotype 21: (0)11(0): (1)8(1): 19: 19: 16: 17: 17: 12: 2T4T3: 2; other females similar. Spermathecae much like those illustrated by Chamberlin (1949: fig. 5A). Chelicera as in male, but a little larger and with slightly longer galeal rami; allotype with an extra seta, like *bs* and *sbs,* on left chelicera. Palp a little shorter and less slender than that of male. L/B of trochanter 1.7–1.75, femur 3.05–3.15, patella 2.45–2.7, and chela (without pedicel) 3.1–3.25; L/D of hand (without pedicel) 2.15–2.2; movable finger L / hand L 0.77–0.80. Fixed finger with 24–27, movable finger with 25–30 teeth. Tarsus of leg I not modified. Subterminal tarsal setae curved and with very small denticulation or apparently acuminate.

Measurements (mm).—*Male:* Figures given first for holotype, followed in parentheses by those for paratype. Body L 2.93 (3.15). Carapace L 0.89 (0.93). Chelicera L 0.28 (0.30). Palp: trochanter 0.43 (0.45)/0.26 (0.27); femur 0.89 (0.96)/0.27 (0.295); patella 0.76 (0.83)/0.295 (0.31); chela (without pedicel) 1.21 (1.33)/0.36 (0.37); hand (without pedicel) 0.67 (0.725)/0.31 (0.325); pedicel L 0.09 (0.10); movable finger L 0.59 (0.665). Leg I: femur 0.30 (0.31)/0.20 (0.19); patella

0.39 (0.40)/0.165 (0.17); tibia 0.38 (0.38)/0.14 (0.15); tarsus 0.34 (0.35)/0.125 (0.13). Leg IV: femur + patella 0.76 (0.79)/0.29 (0.29); tibia 0.56 (0.60)/0.155 (0.155); tarsus 0.39 (0.41)/ 0.11 (0.11).

Female: Ranges for allotype and 2 paratypes. Body L 3.01–4.01. Carapace L 0.925–0.975. Chelicera L 0.295–0.33. Palp: trochanter 0.435/0.25–0.26; femur 0.85–0.95/0.28–0.30; patella 0.73–0.85/0.30–0.315; chela (without pedicel) 1.17–1.22/ 0.36–0.385; hand (without pedicel) 0.68–0.72/0.32–0.325; pedicel L 0.095–0.11; movable finger L 0.525–0.57. Leg I: femur 0.265–0.28/0.16–0.19; patella 0.37-0.42/0.16–0.18; tibia 0.33–0.36/ 0.105–0.13; tarsus 0.30–0.355/0.095–0.105. Leg IV: femur + patella 0.75–0.815/0.27; tibia 0.55–0.585/0.15–0.155; tarsus 0.39–0.42/ 0.11–0.12.

Etymology.—The species is named in honor of Derham Giuliani of Big Pine, Inyo County, California, who collected the type specimens and many other interesting and important pseudoscorpions.

Comments.—It is worth noting that in *Xenochelifer derhami* (and *X. davidi*) the guard setae on each side of the midline on the anterior edge of the posterior genital operculum (sternite 3) in the male are distinctly curved distally and bear a strong lateral spine, sometimes approaching a bifurcate condition. In this respect, they are like many other cheliferid genera, including *Hysterochelifer* (see Hoff 1950: 8, fig. 4). This condition seems to be at variance with the statement by Harvey (1992: 1396, character 112)—"The setae that border the posterior genital operculum of male Lechytiidae are bifurcate, in contrast to those of all other pseudoscorpions."

Chamberlin called special attention to "two slender pseudotactile setae, one subterminal, the other almost median" on the movable finger of the chela of *Xenochelifer davidi* (1949: 11, 15, fig. 4E), and speculated that these 'special' setae were present in correlation with the absence of trichobothria *st* and *sb*. The occurrence of such setae is widespread, if not universal, in the Cheliferoidea; and Vachon (1943) and Boissin (1964) have demonstrated their constancy during nymphal development in *Chelifer cancroides* (Linnaeus) and *Hysterochelifer meridianus* (L. Koch), respectively. I do not believe that the function of these setae has been discussed anywhere in the pseudo-

scorpion literature; but, as Chamberlin pointed out (1949: 12), "these setae are not 'true' tactile setae [trichobothria], as is clear from the nature of the areoles." While the real nature of these setae remains unknown, it is certain that they cannot be viewed as replacements for the missing trichobothria.

LITERATURE CITED

Beier, M. 1963. Ordnung Pseudoscorpionidea. Bestimmungsbücher zur Bodenfauna Europas, Akademie Verlag, Berlin, Germany, 1:1–313.

Benedict, E.M. & D.R. Malcolm. 1979. Pseudoscorpions of the family Cheliferidae from Oregon (Pseudoscorpionida, Cheliferoidea). J. Arachnol., 7:187–198.

Boissin, L. 1964. Remarques sur la morphologie des adultes et des nymphes d'*Hysterochelifer meridianus* (L. Koch) (Arachnides, Pseudoscorpions, Cheliferidae). Bull. Soc. Zool. France, 89: 650–669.

Chamberlin, J.C. 1932. A synoptic revision of the generic classification of the chelonethid family Cheliferidae Simon (Arachnida) (continued). Canadian Entomol., 64:17–21.

Chamberlin, J.C. 1949. New and little-known false scorpions from various parts of the world (Arachnida, Chelonethida), with notes on structural abnormalities in two species. American Mus. Nov., 1430:1–57.

Chamberlin, J.C. 1952. New and little-known false scorpions (Arachnida, Chelonethida) from Monterey County, California. Bull. American Mus. Nat. Hist., 99:259–312.

Harvey, M.S. 1991. Catalogue of the Pseudoscorpionida. Manchester Univ. Press, Manchester, England. 726 pp.

Harvey, M.S. 1992. The phylogeny and classification of the Pseudoscorpionida (Chelicerata: Arachnida). Invert. Taxon., 6:1373–1435.

Hoff, C.C. 1950. Some North American cheliferid pseudoscorpions. American Mus. Nov., 1448:1–18.

Hoff, C.C. 1956. Pseudoscorpions of the family

Cheliferidae from New Mexico. American Mus. Nov., 1804:1–36.

Hoff, C.C. 1958. List of the pseudoscorpions of North America north of Mexico. American Mus. Nov., 1875:1–50.

Muchmore, W.B. 1990. Pseudoscorpionida. Pp. 503–527. *In* Soil Biology Guide. (D.L. Dindal, ed.). John Wiley & Sons, New York.

Vachon, M. 1943. L'allongement des doigts des pinces au cours du développement post-embryonnaire chez *Chelifer cancroides* L. (Pseudoscorpions). Bull. Mus. Natl. d'Hist. Nat., Paris, (2)15:299–302.

RESEARCH NOTE

PHORETIC PSEUDOSCORPIONS ASSOCIATED WITH FLYING INSECTS IN BRAZILIAN AMAZÔNIA

The oldest record of a phoretic association between pseudoscorpions and flying insects in Brazilian Amazônia is that of *Cordylochernes scorpioides* (Linnaeus 1758) traveling under the wings of the cerambycid beetle *Acrocinus longimanus* (Linnaeus 1758) in Belém (Pará State) (Ellingsen 1905). Beck (1968) and Mahnert (1979) reported the same association from Manaus (Amazonas State) and Aguiar & Bührnheim (1992b) extended this occurrence to Rio Branco (Acre State) and mentioned the same pseudoscorpion being transported by another cerambycid species, *Macrodontia cervicornis* (Linnaeus 1758), from Amazonas. Aguiar & Bührnheim (1992b) also recorded *A. longimanus* carrying two other pseudoscorpions, *Parachelifer lativittatus* (Chamberlin 1923) and *Lustrochernes intermedius* (Balzan 1892), in Amazonas. A photograph of *C. scorpioides* under the wings of *A. longimanus* was given by Höfer & Beck (1995).

Recently, other phoretic associations have been reported from several localities in Brazilian Amazônia. Mahnert & Aguiar (1986) described a new pseudoscorpion species, *Neocheiridium triangulare* Mahnert & Aguiar 1986, found associated with a hawkmoth, the sphingid *Cocytius duponchel* (Poey 1932), in Amazonas and Pará. Mahnert (1987) cited *Semeiochernes militaris* Beier 1932 [a synonym of *S. armiger* (Balzan 1892), according to Zeh & Zeh (1992)], being transported by a brachyceran fly, in Pará. Aguiar & Bührnheim (1991) reported the cerambycid beetle, *Stenodontes spinibarbis* (Linnaeus 1758), carrying three pseudoscorpion species, *Lechytia chthoniiformis* (Balzan 1887), *Neocheiridium corticum* (Balzan 1887) and *Lustrochernes intermedius* (Balzan 1892), all from Roraima State (Maracá Island, Uraricoera river). Aguiar & Bührnheim (1992a) studied five pseudoscorpion species, *Tridenchthonius mexicanus* Chamberlin & Chamberlin 1945, *Americhernes* aff. *incertus* Mahnert 1979,

Lustrochernes intermedius, Lustrochernes aff. *reimoseri* Beier 1932 and *Parawithius (V.) gracilimanus* Mahnert 1979 associated with twelve species of passalid beetles, in Amazonas. Moreover, Aguiar et al. (1992) found *Dolichowithius (D.) mediofasciatus* Mahnert 1979, being transported by a species of Platypodidae, *Platypus* sp., in Amazonas; and, more recently, Aguiar et al. (1998), in a study of the occurrence of these Withiidae in wood industries situated in urban areas of Manaus (Amazonas), collected another platypodid, *Platypus parallelus* (Fabricius 1801), also carrying *D. mediofasciatus*. Aguiar & Bührnheim (1998) reported *Parachernes* aff. *albomaculatus* (Balzan 1892) in a phoretic association with an unidentified chrysopid neuropteran from Roraima (Maraca Island). Finally, Mahnert (1979) found *Lustrochernes similis* (Balzan 1892) and *Phymatochernes crassimanus* Mahnert 1979 inside a Malaise trap in Amazonas (Manaus) and Aguiar & Bührnheim (1998) similarly found, in Roraima (Maraca Island), four phoretic pseudoscorpion species in the collecting bottles of several insect traps, their hosts remaining unknown.

The insects and phoretic pseudoscorpions studied here were collected in many different localities of Brazilian Amazonia, the majority in Amazonas State (AM), with some in Acre (AC), Pará (PA) and Rondônia (RO) States (Table 1). They were captured using several collecting techniques, including Malaise trap; Shannon trap; Pennsylvania black light BLB trap; mercury vapor/tungsten light on a white sheet; attraction/interception trap (Aguiar et al. 1992; Aguiar et al. 1998); insect collecting net bag and hand picking. They are lodged in the Entomological Collection of the Universidade do Amazonas. Only the Diptera, Tabanidae and the insects coming from the Jaú National Park (Novo Airão, Amazonas) are lodged in the Invertebrate Collection of the

Table 1.—Pseudoscorpion species in phoretic association with flying insects in the Brazilian Amazonia. * Denotes the first known association between the host and pseudoscorpion species. Abbreviations: AC = Acre State; AM = Amazonas State; PA = Pará State; RO = Rondonia State.

Phoretic pseudoscorpions	Host insects	New geographical distribution data of the association in Amazonia
Chthoniidae		
Lechytia chthoniiformis (Balzan 1890)	Coleoptera, Cerambycidae	
	Stenodontes spinibarbis (L. 1758)	AM (Coari, Tefé, Uarini)
	Stictosomus semicostatus Serville 1832*	AM (Coari)
	Diploschema sp.*	AM (Novo Airão)
Tridenchthoniidae		
Tridenchthonius mexicanus Chamberlin & Chamberlin 1945	Coleoptera, Passalidae	
	Passalus abortivus Percheron 1835*	AM (Novo Airão)
	Passalus aff. *coarctatus* Percheron 1835	
	Passalus convexus Dalman 1817	AM (Coari)
	Passalus elfriedae Luederwaldt 1931	
	Passalus interruptus (L. 1758)	AM (Coari, Itacoatiara, Juruá, Novo Airão)
	Passalus interstitialis Eschscholtz 1829	AM (Coari, Juruá, Novo Airão)
	Passalus latifrons Percheron 1841	
	Passalus (*M.*) *spinifer* Percheron 1841*	AM (Coari)
	Passalus aff. *nasutus* Percheron 1835*	AM (Coari)
	Passalus rhodocanthopoides (Kuwert 1891)	AM (Coari, Juruá)
	Passalus unicornis Lep. & Serv. 1825	AM (Coari)
	Passalus variiphyllus (Kuwert 1891)*	AM (Coari)
	Veturius platyrhinus Westwood 1845	
	Veturius transversus (Dalman 1817)	AM (Coari)
	Unknown host	AM (Carauari, Uarini)
Geogarypidae		
Geogarypus amazonicus Mahnert 1978*	Coleoptera, Cerambycidae	
	Acanthoderes thammi Bates 1880*	AM (Coari)
Atemnidae		
Paratemnoides minor (Balzan 1892)	Homoptera, Cicadidae*	AM (Uarini)
	Coleoptera, Endomychidae*	AM (Manaus)
	Coleoptera, Meloidae: *Epicauta* sp.*	AM (Coari)
	Coleoptera, Cerambycidae: *Styliceps* sp.*	AM (Manaus)
	Coleoptera, Curculionidae: *Cratosomus* sp.*	AM (Manaus)

Table 1.—Continued.

Phoretic pseudoscorpions	Host insects	New geographical distribution data of the association in Amazonia
Cheiridiidae		
Neocheiridium triangulare Mahnert & Aguiar 1986	Lepidoptera, Sphingidae	
	Amphimoea walkeri (Boisduval 1875)*	AM (Coari, São Gabriel da Cachoeira)
	Cocytius anteus (Drury 1773)*	AM (Coari)
	Cocytius duponchel (Poey 1832)	AM (Coari, Itacoatiara, Juruá, Novo Airão, São Gabriel da Cachoeira, Uarini); RO (Porto Velho); AC (Cruzeiro do Sul)
	Isognathus allamandae Clark 1920*	AM (São Gabriel da Cachoeira)
	Isognathus menechus (Boisduval 1875)*	AM (Coari)
Neocheiridium corticum (Balzan 1887)	Coleoptera, Cerambycidae	
Neocheiridium sp.	*Stenodontes spinibarbis* (L. 1758) Hemiptera (Heteroptera), Reduviidae	
	Panstrongylus geniculatus (Latreille 1811)*	AM (Iranduba, Novo Airão)
Chernetidae		
Americhernes aff. *incertus* Mahnert 1979	Coleoptera, Passalidae	
	Passalus aff. *coarctatus* Percheron 1835	
	Passalus convexus Dalman 1917	AM (Coari)
	Passalus elfriedae Luederwaldt 1931	
	Passalus glaberrimus Eschscholtz 1829*	AM (Coari)
	Passalus aff. *nasutus* Percheron 1835*	AM (Coari)
	Passalus unicornis Lep. & Serv. 1825	
	Passalus variiphyllus (Kuwert 1891)	AM (Coari)
	Veturius paraensis Luederwaldt 1927*	AM (Coari, Uarini)
	Veturius platyrhinus Westwood 1845	
Americhernes bethaniae Mahnert 1979*	unknown host	AM (Coari)
Lustrochernes intermedius (Balzan 1892)	Coleoptera, Passalidae	
	Passalus abortivus Percheron 1835*	AM (Novo Airão)
	Passalus interruptus (L. 1758)*	AM (Coari, Novo Airão)
	Passalus interstitialis Eschscholtz 1829	AM (Barcelos, Carauari, Coari, Juruá)
	Passalus rhodocanthopoides (Kuwert 1891)	AM (Coari)
	Paxillus leachi MacLeay 1819*	AM (Uarini)
	Spasalus robustus (Percheron 1835)* Coleoptera, Cerambycidae	AM (Uarini)
	Acrocinus longimanus (L. 1758)	
	Callipogon (*Orthomegas*) sp.*	AM (Coari)
	Macrodontia sp.*	AM (Manaus)
	Stenodontes spinibarbis (L. 1758)	AM (Tefé)

Table 1.—Continued.

Phoretic pseudoscorpions	Host insects	New geographical distribution data of the association in Amazonia
Lustrochernes aff. *reimoseri* Beier 1932	Coleoptera, Passalidae	
	Passalus abortivus Percheron 1835	AM (Novo Airão)
	Passalus aff. *coarctatus* Percheron 1835	
	Passalus convexus Dalman 1817	AM (Coari)
	Passalus elfriedae Luederwaldt 1931	
	Passalus glaberrimus Eschscholtz 1829*	AM (Coari)
	Passalus interruptus (L. 1758)	AM (Coari)
	Passalus interstitialis Eschscholtz 1829	AM (Novo Airão)
	Passalus latifrons Percheron 1841	
	Passalus (*M.*) *spinifer* Percheron 1841*	AM (Coari)
	Passalus aff. *nasutus* Percheron 1835*	AM (Coari)
	Passalus rhodocanthopoides (Kuwert 1891)	
	Passalus unicornis Lep. & Serv. 1825	AM (Coari)
	Passalus variiphyllus (Kuwert 1891)	AM (Juruá)
	Popilius marginatus (Percheron 1835)*	AM (Coari)
	Popilius tetraphyllus (Eschscholtz 1829)*	AM (Tefé)
	Veturius platyrhinus Westwood 1845	
	Veturius transversus (Dalman 1817)	AM (Coari)
	Veturius sp.*	AM (Coari)
	Verres furcilabris (Eschscholtz 1829)	
Lustrochernes similis (Balzan 1892)	Coleoptera, Cerambycidae	
	Acanthoderes thammi Bates 1880*	AM (Coari)
	Steirastoma melanogulys Withe 1855*	AM (Coari, Novo Airão, Presidente Figueiredo, Uarini)
	Compsibidion maronicum (Thomson 1867)*	AM (Manaus)
Cordylochernes scorpioides (L. 1758)	Coleoptera, Cerambycidae	
	Acrocinus longimanus (L. 1758)	AM (Juruá, Novo Airão, São Gabriel da Cachoeira, Tefé)
	Macrodontia cervicornis (L. 1758)	AM (Itacoatiara)
	Titanus giganteus (L. 1771)*	AM (Manaus)
Parachernes adisi Mahnert 1979	unknown host	AM (Guajará)
Parachernes aff. *adisi* Mahnert 1979	unknown host	AM (Coari)
Parachernes aff. *albomaculatus* (Balzan 1892)	Neuroptera, Chrysopidae	
	unknown host	AM (Tefé)

Table 1.—Continued.

Phoretic pseudoscorpions	Host insects	New geographical distribution data of the association in Amazonia
Parachernes inpai Mahnert 1979*	Diptera, Culicidae*	AM (Novo Airão)
	Diptera, Tabanidae	
	Phorcotabanus cinereus (Wiedemann 1821)*	AM (Manaus)
	Tabanus occidentalis L. 1758*	PA (Monte Alegre)
Parachernes melano-pygus Beier 1959*	Diptera, Tabanidae	
	Phorcotabanus cinereus (Wiedemann 1821)*	AM (Manaus)
	Stenotabanus cretatus Fairchild 1961*	AM (Manaus)
	Tabanus amapaensis Fairchild 1961*	AM (Manaus)
	unknown host	AM (Manaus); RO (Ariquemes)
Parachernes plumosus (White 1908)*	Diptera, Tabanidae	
	Phorcotabanus cinereus (Weidemann 1821)*	AM (Manaus)
	Stenotabanus cretatus Fairchild 1961*	AM (Novo Airão)
	Tabanus trivittatus Fabricius 1805*	AM (Uarini)
Phymatochernes crassimanus Mahnert 1979	unknown host	AM (Carauari, Coari)
Semeiochernes armiger (Balzan 1892)	Diptera, Pantophthalmidae	
Parazaona sp.	Hemiptera (Heteroptera), Reduviidae	
	Panstrongylus geniculatus (Latreille 1811)*	AM (Novo Airão)
Withiidae		
Parawithius (V.) gracilimanus Mahnert 1979	Coleoptera, Passalidae	
	Passalus elfriedae Luederwaldt 1931	
	Passalus interruptus (L. 1758)	
	Passalus interstitialis Eschscholtz 1829	
	Passalus rhodocanthopoides (Kuwert 1891)	
	Passalus unicornis Lep. & Serv. 1825	
	Unknown host	AC (Rio Branco)
Parawithius sp.	Hemiptera (Heteroptera), Reduviidae	
	Caridomma sp.*	AM (Itacoatiara)
Dolichowithius (D.) mediofasciatus Mahnert 1979	Coleoptera, Platypodidae	
	Platypus parallelus (Fabricius 1801)	AC (Plácido de Castro)
	Platypus sp.	AC (Plácido de Castro)
	unknown host	AM (Coari, São Sebastião do Uatumã)
Dolichowithius (D.) aff. *longichelifer* (Balzan 1887)*	unknown host	AM (Coari)

Table 1.—Continued.

Phoretic pseudoscorpions	Host insects	New geographical distribution data of the association in Amazonia
Cacodemonius sp. 1	Coleoptera, Cerambycidae	
	Callipogon (*Orthomegas*) sp.*	AM (Coari)
	Coleoptera, Passalidae	
	Passalus rhodocanthopoides (Kuwert 1891)*	AM (Coari)
Cacodemonius sp. 2	Coleoptera, Passalidae	
	Passalus abortivus Percheron 1835*	AM (Novo Airão)
	Passalus punctiger Lep. & Serv. 1825*	AM (Coari)
	Paxillus leachi MacLeay, 1819*	AM (Coari)
	Coleoptera, Cerambycidae	
	Stenodontes spinibarbis (L. 1758)*	AM (Coari, Tefé, Uarini)
	Callipogon (*Orthomegas*) sp.*	AM (Coari)
Cheliferidae		
Parachelifer lativittatus (Chamberlin 1923)	Coleoptera, Cerambycidae *Acrocinus longimanus* (L. 1758)	AM (Juruá, Novo Airão, São Gabriel da Cachoeira, Tefé, Uarini)

Instituto Nacional de Pesquisas da Amazônia (INPA).

Phoretic associations with flying insects were found in 19 of the 64 described pseudoscorpion species that are known to occur in the Brazilian Amazonia (Harvey 1991), along with 10 other morphospecies, which are presumably undescribed. Twenty four of these species were found with 56 insect species, belonging to five orders (Hemiptera, Neuroptera, Coleoptera, Lepidoptera and Diptera); and the remaining five species were associated with unknown hosts, since they were found free in flying insects traps, probably brought by some of the countless insects collected. Only more detailed studies will allow us to ascertain the host insect species.

The Coleoptera proved to be the most frequent insect carriers of pseudoscorpions in the Amazonian region, representing 40 of the 56 host species (Table 1). The 23 species of passalid beetles collected were each found to carry as many as five pseudoscorpion species, and individual hosts sometimes carried three pseudoscorpion species, one on the pronotum and the others under the wings (Aguiar & Bührnheim 1992a). Twelve species of cerambycid beetles were found to carry pseudoscorpions, some of which were involved with the regular phoretic transport of certain pseudoscorpions, such as *Acrocinus longimanus,*

frequently carrying both *Cordylochernes scorpioides* under the wings and *Parachelifer lativittatus* behind the pronotal lateral spine (Aguiar & Bührnheim 1992b). Another cerambycid beetle, *Stenodontes spinibarbis,* was found to carry four pseudoscorpion species, sometimes with three species under the wings of a single host (Aguiar & Bührnheim 1991). A third cerambycid beetle, *Steirastoma melanogulys* White 1855, was observed for the first time to be carrying *Lustrochernes similis* gripped to the third antennal segment (first segment of the antennal flagellum), a mode of transport found to be quite frequent. Platypodid beetles proved to be important carriers of *Dolichowithius (D.) mediofasciatus* (Aguiar et al. 1992; Aguiar et al. 1998). Many of the host beetles, such as Passalidae and Cerambycidae, are inhabitants of fallen rotting trunks and, not surprisingly, many of the pseudoscorpions that they carry also live in this environment (Mahnert & Adis 1985).

Among the Lepidoptera, five species of Sphingidae were found carrying only *Neocheiridium triangulare. Cocytius duponchel* (Poey 1832) was the most common carrier of this pseudoscorpion species, whose habitat has not yet been discovered.

Amongst the Diptera, the Tabanidae were represented by five species carrying three pseudoscorpions: *Parachernes plumosus*

(With 1908) was always found attached to an abdominal tergite, whereas *P. inpai* Mahnert 1979 and *P. melanopygus* Beier 1959 were always found attached to the hind legs of the host. These pseudoscorpion species were never found sharing the same fly, and individuals were always alone on each fly. Other host Diptera included a culicid carrying *P. inpai,* a forest canopy inhabitant, and a pantophtalmid, reported only as Diptera by Mahnert (1987), carrying nine individuals of *Semeiochernes militaris* (= *S. armiger*) on the same host specimen.

Some Hemiptera were also found carrying pseudoscorpions, including an unidentified Cicadidae (Homoptera) carrying *Paratemnoides minor* (Balzan 1892), a bark tree-trunk inhabitant, and two Reduviidae (Heteroptera), one Triatominae, *Panstrongylus geniculatus* (Latreille 1811), which occurred once carrying *Neocheiridium* sp. and on another occasion, carrying *Parazaona* sp., as well as a species of Cetherinae, *Caridomma* sp., carrying an unidentified species of *Parawithius.*

In some of the more frequent associations studied, nymphal pseudoscorpions were found in phoretic associations as frequently as adult males and females (Mahnert & Aguiar 1986; Aguiar et al. 1992; Aguiar & Bührnheim 1992a).

Future studies on the phoretic behavior of these arachnids are clearly warranted, especially of the associations that occur frequently. New associations undoubtedly remain to be discovered, since our knowledge of Amazonian pseudoscorpions needs to be extended to cover larger geographical and environmental ranges. There is also a lack of natural history studies of the host insects and their phoretic pseudoscorpions in Amazonia. When these studies are undertaken, it should help elucidate the relationships of these arthropod populations.

LITERATURE CITED

Aguiar, N.O. & P.F. Bührnheim. 1991. Pseudoscorpiões foréticos de *Stenodontes spinibarbis* (Lin. 1758) (Coleoptera) e redescrição de *Lechytia chthoniiformis* (Balzan, 1890) (Pseudoscorpiones, Chthoniidae) da Ilha de Maracá - Roraima. Acta Amazônica, 21:425–433.

Aguiar, N.O. & P.F. Bührnheim. 1992a. Pseudoscorpiones (Arachnida) em associação forética com Passalidae (Insecta, Coleoptera) no Amazonas, Brasil. Amazoniana, 12:187–205.

Aguiar, N.O. & P.F. Bührnheim. 1992b. Pseudoscorpiões foréticos de Cerambycidae (Coleoptera) e ocorrência de *Parachelifer lativittatus* Chamberlin, 1932 (Pseudoscorpiones, Cheliferidae) na Amazônia. Bol. Mus. Emílio Goeldi, sér. Zool., 8:343–348.

Aguiar, N.O. & P.F. Bührnheim. 1998. Pseudoscorpions (Arachnida) of the Ilha de Maracá. Pp. 381–389. *In* Maracá: The Biodiversity and Environment of a Rainforest. (Milliken & Ratter, eds.). John Wiley & Sons Ltd. England.

Aguiar, N.O., J. Vicente-da-Silva & P.F. Bührnheim. 1992. *Dolichowithius mediofasciatus* Mahnert, 1979 (Arachnida, Pseudoscorpiones, Withiidae) em forésia com Platipodidae (Insecta, Coleoptera), no Amazonas, Brasil. Amazoniana, 12:181–185.

Aguiar, N.O., A.M.R. Arruda & P.F. Bührnheim. 1998. Pseudoscorpiones (Arachnida) em dispersão por forésia sobre insetos voadores, em indústrias madeireiras de Manaus, Amazonas. Revta Univ. Amazonas, Sér. Ciênc. Agrárias, 6 (1):79–89.

Beck, L. 1968. Aus den Regenwäldern am Amazonas I. Natur und Museum, 98:24–32.

Ellingsen, E. 1905. Pseudoscorpions from South America. Collected by A. Borelli, A. Bertoni de Winkelried, and Prof. Goeldi. Boll. Mus. Zool. Anat. Comp. R. Univ. Torino, 20 (500): 1–17.

Harvey, M.S. 1991. Catalogue of the Pseudoscorpionida. (V. Mahnert, ed.) Manchester University Press, Manchester.

Höfer, H. & L. Beck. 1995. Die Spinnentierfauna des Regenwaldreservats ''Reserva Ducke'' in Zentralamazonien I. Natur und Museum, 125: 389–401.

Mahnert, V. 1979. Pseudoskorpione (Arachnida) aus dem Amazonas-Gebiet (Brasilien). Rev. Suisse Zool., 86:719–810.

Mahnert, V. 1987. Neue oder wenig bekannt, vorwiegend mit Insekten vergesellschaftete Pseudoskorpione (Arachnida) aus Südamerika. Mittlg. Schweizerischen Entomol. Ges., 60: 403–416.

Mahnert, V. & J. Adis. 1985. On the occurrence and habitat of Pseudoscorpiones (Arachnida) from Amazonian forest of Brasil. Stud. Neotrop. Fauna Environ., 20:211–215.

Mahnert, V. & N.O. Aguiar. 1986. Wiederbeschreibung von *Neocheiridium corticum* (Balzan, 1890) und Beschreibung von zwei neuen Arten der Gattung aus Südamerika (Pseudoscorpiones, Cheiridiidae). Mittlg. Schweizerischen Entomol. Ges., 59:499–509.

Zeh, D.W. & J.A. Zeh. 1992. Emergence of a giant fly triggers phoretic dispersal in the neotropical pseudoscorpion, *Semeiochernes armi-*

ger (Balzan) (Pseudoscorpionida: Cherneti-dae). Bull. British Arachnol. Soc., 9:43–46.

Nair Otaviano Aguiar and **Paulo Friedrich Bührnheim**: Universidade do Amazonas, Institute of Biological Sciences, Department of Biology, Lab. of Zoology, Av. Gal. Rodrigo Octavio Jordão Ramos, 3000 - 69.077–000 Manaus, Amazonas, Brazil.

ARACHNOLOGICAL RESEARCH FUND

The AAS Fund for Arachnological Research (AAS Fund) is funded and administered by the American Arachnological Society. The purpose of the fund is to provide research support for work relating to any aspect of the behavior, ecology, physiology, evolution, and systematics of any of the arachnid groups. Awards may be used for field work, museum research (including travel), expendable supplies, identification of specimens, and/or preparation of figures and drawings for publication. Monies from the fund are not designed to augment or replace salary.

Individual awards will not exceed $1000.00, and, although open to all students and faculty with less than $500.00 per year research budget, preference will be given to students. A total of $6000.00 is available for awarding during each funding year. Available monies could be expended for three large proposals, a greater number of partially funded proposals, and/or a number of smaller, less expensive proposals. The final funding pattern is at the discretion of the review committee.

Applications for support should be received by the chair of the review committee no later than October 31. To be considered for an award from the AAS Fund, please submit four copies of a proposal of no more than five pages (including references) detailing your research project.

Proposals should have three main parts: 1) an INTRODUCTION where background information is presented relative to the proposed work. The introduction should include a section which places the proposed work in context with currently known relevant information, a section which provides justification for the proposed work, and a clear statement of the hypothesis(ses) to be tested, or, in the case of systematic revisions, the type of synthesis that will be achieved and its significance; 2) a METHODS section where the methods, materials, experimental design, and statistical or taxonomic analysis(ses) to be used are clearly and concisely presented, and 3) a BUDGET explaining (in detail) how monies awarded will be spent in the proposed research.

Proposals should be submitted to:

Dr. Deborah Smith, AAS Fund Chair
Department of Entomology
Haworth Hall
University of Kansas
Lawrence, KS 66045 USA

Proposals must be submitted in English. The four copies of the proposal must be in the hands of the Fund chair by the appropriate deadlines to be considered. Electronic submission and/or FAX submission of proposals with hard copies to follow is acceptable only if the other copies arrive before the stated deadlines. If these submission rules are difficult or prohibitive because of cost, erratic postal services, or remote location (remote field stations or sites), other methods of submission may be acceptable. For other submission possibilities, please contact the chair of the Fund at the above address, or electronically at dsmith@kuhub.cc.ukans.edu. Alternative submissions will be accepted only if the chair has been previously contacted, and all deadlines will still apply.

INSTRUCTIONS TO AUTHORS

(revised October 1996)

Manuscripts are preferred in English but may be accepted in Spanish, French or Portuguese subject to availability of appropriate reviewers. Authors whose primary language is not English may consult the Associate Editor for assistance in obtaining help with English manuscript preparation. All manuscripts should be prepared in general accordance with the current edition of the *Council of Biological Editors Style Manual* unless instructed otherwise below. Authors are advised to consult a recent issue of the *Journal of Arachnology* for additional points of style. Manuscripts longer than 1500 words should be prepared as Feature Articles, shorter papers as Research Notes. Send **four** identical copies of the typed material together with photocopies of illustrations to the **Managing Editor**. Do not send original handmade illustrations until the manuscript has been accepted. Mail to:

Petra Sierwald, Managing Editor; Division of Insects, Dept. of Zoology, Field Museum, Roosevelt Road at Lakeshore Drive, Chicago, IL 60605 USA [Telephone: (312) 922-9410, ext. 841; FAX: (312) 663-5397; E-mail: SIERWALD@FMNH.ORG]

Correspondence relating to the initial submission of a manuscript, as well as the review process, should be directed to the Associate Editor. Correspondence relating all other matters should be directed to the Editor. After the manuscript has been accepted, the author will be asked to submit the manuscript on a computer disc. It must be in a widely used program (preferably in MS DOS WordPerfect). Indicate clearly on the computer disc the word processing program used.

FEATURE ARTICLES

Title page.—The title page will include the complete name, address, and telephone number of the author with whom proofs and correspondence should be exchanged, a FAX number and electronic mail address if available, the title in capital letters, and each author's name and address, and the running head (see below).

Abstract.—The heading in capital letters should be placed at the beginning of the first paragraph set off by a period. In articles written in English, a second abstract in an acceptable language may be included pertinent to the nationality of the author(s) or geographic region(s) emphasized in the article. A second abstract in English must be included in articles not written in the latter language.

Text.—Double-space text, tables, legends, etc. throughout. Three levels of heads are used. The first level (METHODS, RESULTS, etc.) is typed in capitals and on a separate line. The second level head begins a paragraph with an indent and is separated from the text by a period and a dash. The third level may or may not begin a paragraph but is italicized and separated from the text by a colon. Use only the metric system unless quoting text or referencing collection data. All decimal fractions are indicated by the period regardless of language of the text.

Citation of references in the text: Cite only papers already published or in press. Include within parentheses the surname of the author followed by the date of publication. A comma separates multiple citations by the same author(s) and a semicolon separates citations by different authors, e.g., (Smith 1970), (Jones 1988; Smith 1993), (Smith 1986, 1987; Smith & Jones 1989; Jones et al. 1990).

Literature cited section.—Use the following style:

Lombardi, S. J. & D. L. Kaplan. 1990. The amino acid composition of major ampullate gland silk (dragline) of *Nephila clavipes* (Araneae, Tetragnathidae). J. Arachnol., 18:297–306.
Krafft, B. 1982. The significance and complexity of communication in spiders. Pp. 15–66, *In* Spider

Communications: Mechanisms and Ecological Significance. (P. N. Witt & J. S. Rovner, eds.). Princeton University Press, Princeton, New Jersey.

Footnotes.—Footnotes are permitted only on the first printed page to indicate current address or other information concerning the author. All footnotes are placed together on a separate manuscript page.

Running head.—The author surname(s) and an abbreviated title should be typed all in capital letters and must not exceed 60 characters and spaces. The running head should be placed near the top of the title page.

Taxonomic articles.—Consult a recent taxonomic article in the *Journal of Arachnology* for style or contact the Editor.

Tables.—Each table, with the legend above, should be placed on a separate manuscript page. Only horizontal lines (usually three) should be included. Use no footnotes; instead, include all information in the legend. Make notations in the text margins to indicate the preferred location of tables in the printed text.

Illustrations.—Address all questions concerning illustrations to:

James W. Berry, Editor-In-Chief; Dept. of Biological Sciences, Butler University, Indianapolis, Indiana 46208 USA [Telephone (317) 940-9344; FAX (317) 940-9519; E-mail: jwberry@thomas.butler.edu]

All art work must be camera-ready for reproduction. In line drawings, pay particular attention to width of lines and size of lettering when reductions are to be made by the printer. Multiple photos assembled on a single plate should be mounted with only a minimum of space separating them. In the case of multiple illustrations mounted together, each illustration must be numbered sequentially rather than given an alphabetic sequence. Written on the back should be the name(s) of author(s) and an indication of top edge. The author should indicate whether the illustrations should be one column or two columns in width. The overall dimensions of original artwork should be no more than 11 inches (28 cm) × 14 inches (36 cm). Photocopies in review manuscripts should be reduced to the exact measurements that the author wants to appear in the final publication. Larger drawings present greater difficulty in shipping and greater risks of damage for which the JOA assumes no responsibility. Make notations in the text margins to indicate the preferred position of illustrations in the printed text.

Legends for illustrations should be placed together on the same page(s) and separate from the illustrations. Each plate must have only one legend, as indicated below:

Figures 1–4.—*A-us x-us*, male from Timbuktu. 1, Left leg; 2, Right chelicera; 3, Dorsal aspect of genitalia; 4, Ventral aspect of abdomen.

Figures 27–34.—Right chelicerae of species of *A-us* from Timbuktu. 27, 29, 31, 33, Dorsal views; 28, 30, 32, 34, Prolateral views of moveable finger; 27, 28, *A-us x-us*, holotype male; 33, 34, *A-us y-us*, male. Scale = 1.0 mm.

Assemble manuscript for mailing.—Assemble the separate sections or pages in the following sequence: title page, abstract, text, figure legends, footnotes, tables with legends, figures.

Page charges, proofs and reprints.—There are no page charges, but authors will be charged for changes made in the proof pages. Authors will receive a reprint order form along with their page proofs. Reprints will be billed at the printer's current schedule of costs.

RESEARCH NOTES

Instructions above pertaining to feature articles apply also to research notes, except that abstracts and most headings are not used and the author's name and address follow the Literature Cited section.

CONTENTS

The Journal of Arachnology